

Selection Strategies of Parasitized Hosts in a Generalist Parasitoid Depend on Patch Quality but Also on Host Size

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*Host rejection, superparasitism, and ovicide are three possible host selection strategies that parasitoid females can adopt when they encounter parasitized hosts. These differ in costs (in terms of time and energy required) and benefits (in terms of number and quality of offspring produced). Their relative payoff should vary with patch quality, (i.e., proportion of parasitized hosts present), and female choice between them should be adapted accordingly. We conducted behavioral observations to test the effect of the ratio of parasitized/unparasitized hosts present in a patch on the host selection strategies of *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae). This species being a generalist known to attack hosts of a great range of size, we also tested the impact of host size on female decisions with two host species differing greatly in size (*Drosophila melanogaster* and *Delia radicum*). We evaluated the adaptive value of each strategy in relation to host parasitization status and host size by measuring their duration and the potential number of offspring produced.*

KEY WORDS: patch quality; host quality; ovicide; superparasitism; self-superparasitism; behavior.

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INTRODUCTION

Contrary to prey eaten by predators, hosts parasitized by female parasitoids remain in the habitat and can be encountered again by other foraging females. When encountering such hosts, females can choose between two classical strategies: reject them and look for more suitable hosts or accept them and lay a second egg or clutch of eggs on these already parasitized hosts (i.e., superparasitize them). A third strategy is available in some species, where females are able to kill the eggs already present on or in the hosts (i.e., perform ovidicides) before parasitizing them. They can achieve this either by piercing the eggs with their ovipositor (Price, 1970; Arakawa, 1987; van Alebeek *et al.*, 1993; Antolin *et al.*, 1995), eating them (Goertzen and Doult, 1975; Hardy and Blackburn, 1991; Mayhew, 1997), or injecting a toxic substance to the first egg at the moment of oviposition (Mackauer, 1991). Ovidicide is rarely reported but it could be greatly underestimated in parasitoids due to the difficulty to observe it (Strand and Godfray, 1989; Netting and Hunter, 2000). These three strategies differ in costs (in terms of time and energy required) and benefits (in terms of number and quality of offspring produced) and strongly impact female fitness. The choice among the three strategies are known to depend on the quality of the patches encountered by the females in terms of ratio of parasitized/unparasitized hosts present (Strand and Godfray, 1989; van Alphen and Visser, 1990). Indeed, when unparasitized hosts are frequent, the *rejection* of parasitized hosts should be more frequent since it allows investing more time and energy into the search and exploitation of more profitable hosts (van Lenteren, 1981). This, however, depends on female physiological state: time-limited females should switch to superparasitism earlier (Sirot *et al.*, 1997). Then, when the patch is depleted (i.e., when unparasitized hosts become less frequent), *superparasitism* becomes more adaptive, especially when the survival chances of a second clutch are high (van Alphen and Visser, 1990). To enhance the probability of obtaining an offspring in such conditions, it can be interesting to deposit more than one egg (i.e., *self-superparasitism*) in the same parasitized host because it can increase the probability that the winner of the larval competition will be an offspring of the superparasitizing female. Therefore, the payoff from self-superparasitism increases with the intraspecific competition level (Visser *et al.*, 1992). The adaptiveness of superparasitism also depends on the egg-limitation status of the females. As in the case of superparasitism, *ovicide* appears to be advantageous when unparasitized hosts are scarce but its evolution should be favored when the survival chances of a second clutch are low, the travel time between hosts is long (Strand and Godfray, 1989), and the risk for a female to kill its own eggs is reduced (Smith and Lessels, 1985). However, an important constraint seems to refrain the occurrence

of ovicide: the time needed and the difficulty to find and reach eggs to destroy (Netting and Hunter, 2000). Therefore, its occurrence may be greatly influenced by host size: smaller hosts may allow for a shorter handling time (Schmidt and Smith, 1987; King, 1994) and provide better opportunities to perform ovicides because eggs from competing females may be easier to detect (Netting and Hunter, 2000).

We determined the influence of patch quality, measured as the proportion of parasitized hosts present, on the strategies (host rejection, superparasitism or ovicide) displayed by *Pachycrepoideus vindemmiae* (=dubius) Rondani (Hymenoptera: Pteromalidae), a generalist solitary parasitoid (Crandell, 1939). Previous experiments have shown that this parasitoid is able to discriminate parasitized hosts from unparasitized ones (Nell and van Lenteren, 1982; Goubault *et al.*, 2004) and perform ovicides (Nell and van Lenteren, 1982). *P. vindemmiae* is known to parasitize the pupae of many cyclorrhaphous dipteran species differing greatly in size (Nostvik, 1954): it has been found on *Drosophila melanogaster* L. (Diptera: Drosophilidae), whose pupae do not exceed 3 mm in length, and also on *Calliphora* sp., whose pupae can reach 14 mm in length (Rueda and Axtell, 1985). Therefore, we also tested whether host size influenced the decisions, regarding parasitized hosts, made by females of this parasitoid. For that purpose, we chose two host species at the two extremes of the host-size range of *P. vindemmiae*: a small one, *D. melanogaster*, and a bigger one, *Delia radicum* L. (Diptera: Anthomyiidae). *D. radicum* is twice as long and about eight times bigger in volume than *D. melanogaster*. We assessed the adaptive value of each strategy in relation with host quality (parasitization status and host size) by quantifying the time cost of female behavioral decisions and the potential number of offspring obtained in each case.

MATERIALS AND METHODS

Rearing

The first host species, *D. radicum*, originated from pupae collected from cabbage fields (Le Rheu, Brittany, France) in 1994. It was reared in the laboratory on rutabaga roots (*Brassica napus* L.) at $20 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH, and 16L:8D as described by Neveu *et al.* (1996).

The second host species, *Drosophila melanogaster* Meig, was provided by R. Allemand (Université de Lyon, 2000). It was reared on an anoxic medium (David, 1962) at $25 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH, and 16L:8D).

The *P. vindemmiae* strain was collected in Rennes (Brittany, France) in 2000 and was reared on pupae of *D. radicum* under the same climatic

conditions as *D. melanogaster*. Adults were maintained in petri dishes ($\phi = 8.5$ cm; $h = 2.7$ cm) and supplied with honey, water, and about 150 host pupae, which were replaced three times a week. Parasitized pupae were stored in petri dishes under the same climatic conditions until the emergence of new adults.

Experimental Procedures

The *P. vindemmiæ* females used in all experiments were 24 h old and fed with honey. Prior to testing, they were mated and experienced with the same host species that they would be confronted to during the test (either *D. radicum* or *D. melanogaster* pupae). For that purpose, females were individually placed in the presence of one male and five unparasitized pupae during 13 h. Females were then placed in empty petri dishes for at least 1 h. Preliminary tests have shown that 90% of the females submitted to such conditions were mated and had at least one oviposition experience. All experiments were performed at $22 \pm 1^\circ\text{C}$ and $40 \pm 10\%$ RH.

The *D. radicum* pupae (6 mm long) used in our tests were 7 to 9 days postpupation, the optimal age for *P. vindemmiæ* (Grandgirard *et al.*, 2002). The *D. melanogaster* pupae (3 mm long) were 1–2 days old, following van Alphen and Thunissen (1983). Unparasitized and parasitized hosts were used in the experiments. When parasitized hosts were used, they were parasitized by conspecific females 0–4 h before the experiments.

Female Strategies

To determine which oviposition decisions concerning parasitized hosts are made by females according to patch quality and host size and estimate the costs and benefits of each of these strategies, we examined the behavior of females placed individually in petri dishes ($\phi = 8.5$ cm; $h = 2.7$ cm) under two patch conditions:

- (1) *Medium-quality patch*. Each female was presented with five unparasitized hosts and five parasitized hosts (*D. radicum* hosts, $N = 27$; *D. melanogaster* hosts, $N = 14$). The position of each type of host was alternated in the petri dishes so that females had the same probability of encountering both types.
- (2) *Poor-quality patch*. Each female was presented with 10 parasitized hosts (*D. radicum* hosts, $N = 28$; *D. melanogaster* hosts, $N = 14$).

After the departure of females from a host the ones drilled during the experiments were immediately replaced by hosts of the same type in order to keep the patch quality constant. This avoided possible confounding effects between initial patch quality and change in patch quality due to gradual depletion.

The behavior of each female was recorded using a video camera mounted on a binocular and connected to a monitor. Using a program for behavioral data collection (THE OBSERVER [Noldus, 1991]), the following behavioral items were recorded for 2 h: host encounter, host rejection, and host acceptance (oviposition of either a single egg or two eggs, with or without ovicide). Hosts were dissected at the end of the test to count the eggs laid and the state of these eggs (either normal or punctured). Punctured eggs correspond to egg's chorions emptied from their contents after females have pierced them with their ovipositor. Acceptation rate was calculated as the percentage of encountered hosts on which at least one egg was laid. Among accepted hosts, the percentages of single ovipositions, double ovipositions, and ovicides were calculated. The rates of occurrence of each strategy according to patch and host quality were compared by chi-square tests or Fisher's exact tests (when the number of observations was lower than five).

Costs and Benefits of Strategies

The time cost of each strategy was evaluated by measuring the time necessary to handle the host (i.e., from the first contact until the departure from the host). When females accepted a host, the handling sequence was divided into four steps: initial external exploration (females examine the host externally by drumming its surface with their antennae and then tapping it with the tip of their ovipositor sheath), drilling, probing (including oviposition), and final external exploration (females examine the host externally again before leaving it). When females accepted parasitized hosts, we checked whether or not they reused the oviposition holes previously drilled by conspecific females. Durations of behavioral items were compared by *t*-tests or ANOVA tests followed by Fisher's PLSD.

To estimate the relative fitness gain provided by the different strategies where parasitized hosts were accepted, the number of potential offspring gained per hour was calculated. For this, we allocated a gain of 0.5 offspring when an egg was deposited in a parasitized host, as each individual has a similar probability of winning the larval competition when the time interval between ovipositions is only 0–4 h (Goubault *et al.*, 2003). When females deposited two eggs in the same parasitized host, we allocated a gain of 0.33

to each egg. In the case of an ovicide, we simplified by considering that the initial host quality was completely restored and allocated a gain of 1. Then, for each strategy, total gains were divided by the total host handling time, thus giving a mean gain per hour. Thanks to this transformation, the results could be compared to each other. Potential number of offsprings gained from the different strategies were compared by ANOVA tests followed by Fisher's PLSD on *D. radicum* (where single and double ovipositions occurred with or without ovicide) and *t*-tests on *D. melanogaster* (where only single ovipositions occurred with or without ovicide).

RESULTS

Female Strategies

Host Acceptance

In medium-quality patches, *P. vindemniae* females accepted significantly fewer parasitized hosts than unparasitized hosts on both host species (*D. radicum*, $\chi^2 = 8.47$, $df = 1$, $P = 0.004$; *D. melanogaster*, $\chi^2 = 21.06$, $df = 1$, $P < 0.0001$) (Fig. 1A). In poor patches, the acceptance rate of parasitized *D. radicum* pupae was similar to the acceptance rate observed in medium-quality patches ($\chi^2 = 0.44$, $df = 1$, $P = 0.51$) (Fig. 1A). On *D. melanogaster* pupae, on the contrary, the acceptance rate of parasitized hosts was higher in poor-quality patches than in medium quality patches ($\chi^2 = 7.54$, $df = 1$, $P = 0.006$, Fig. 1A). In all cases, acceptance rates were significantly higher on *D. radicum* (medium-quality patches—unparasitized hosts, $\chi^2 = 35.41$, $df = 1$, $P < 0.0001$; parasitized hosts, $\chi^2 = 52.39$, $df = 1$, $P < 0.0001$; poor-quality patches— $\chi^2 = 31.26$, $df = 1$, $P < 0.0001$) (Fig. 1A).

Parasitism/Superparasitism

The number of eggs laid varied with the parasitization status of hosts. Single ovipositions were more frequent in unparasitized than parasitized hosts in medium-quality patches (*D. radicum*, $96.3 \pm 2.1\%$ in unparasitized hosts [$N = 81$] vs. $84.1 \pm 4.6\%$ in parasitized hosts [$N = 63$], $\chi^2 = 6.39$, $df = 1$, $P = 0.01$; *D. melanogaster*, $100.0 \pm 0.0\%$ in unparasitized hosts [$N = 71$] vs. $89.7 \pm 3.6\%$ in parasitized hosts [$N = 29$], Fisher's exact test, $P = 0.02$). In medium-quality patches, the proportion of single ovipositions in accepted parasitized hosts was similar in both host species (Fisher's exact test, $P = 0.36$).

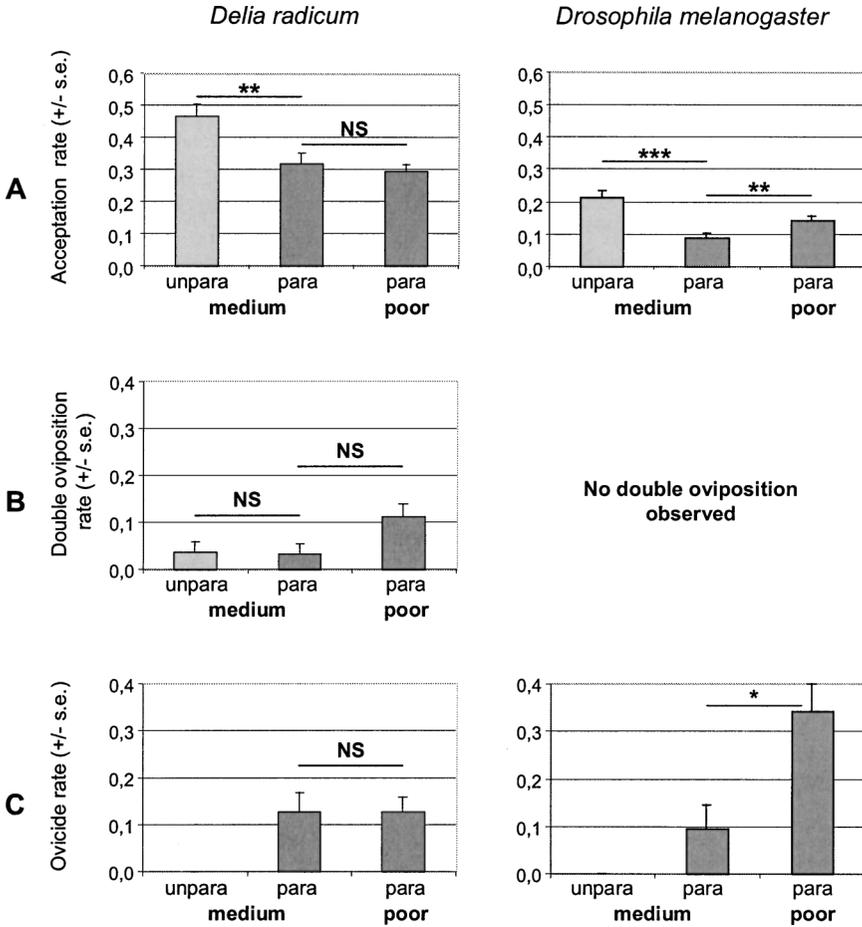


Fig. 1. Acceptation rate of encountered hosts (A), double oviposition rate (B), and ovicide rate (C) of accepted hosts. Results concern two host species, *Delia radicum* and *Drosophila melanogaster*. Two qualities of patch were tested: (i) “medium”-quality patches, where 50% of hosts were already parasitized (=para) and the other were unparasitized (=unpara), and (ii) “poor”-quality patches, where 100% of hosts were already parasitized. NS, nonsignificant difference; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Double ovipositions (i.e., self-superparasitism) were only observed on *D. radicum*. On this host species, the rate of double ovipositions was not influenced by the parasitization status of hosts (case of medium quality patch) (Fisher’s exact test, $P = 0.62$). Nevertheless, double ovipositions in parasitized hosts were slightly, but not significantly, more frequent in poor-than in medium-quality patches ($\chi^2 = 3.47$, $df = 1$, $P = 0.06$) (Fig. 1C).

Ovicide

On *D. radicum*, the rate of ovicide was similar in poor and medium-quality patches ($\chi^2 < 0.0001$, $df = 1$, $P = 0.98$), whereas on *D. melanogaster*, the rate of ovicide was higher in poor-than in medium-quality patches ($\chi^2 = 5.93$, $df = 1$, $P = 0.02$) (Fig. 1B). In medium-quality patches, the frequency of ovicide was similar in both host species (Fisher's exact test, $P = 0.52$), whereas in poor-quality patches, it was higher on *D. melanogaster* than on *D. radicum* ($\chi^2 = 12.70$, $df = 1$, $P < 0.0001$) (Fig. 1B).

Costs and Benefits of Strategies

Time Cost of Strategies

All 18 ovidices recorded on *D. radicum* occurred while females were reusing the oviposition hole previously drilled through the puparium by conspecific females. In contrast, only 14 ovidices of 26 were performed this way on *D. melanogaster*, the 12 others involving the drilling of a new hole (difference between host species: $\chi^2 = 14.22$, $df = 1$, $P < 0.0001$).

Durations in both experiments involving parasitized hosts (medium- and poor-quality patches) did not differ significantly and were pooled. The durations of initial and final external explorations were similar on unparasitized and parasitized hosts in both species (initial—*D. radicum*, $F = 1.98$, $P = 0.12$; *D. melanogaster*, $F = 0.10$, $P = 0.98$; final—*D. radicum*, $F = 0.83$, $P = 0.48$; *D. melanogaster*, $F = 0.44$, $P = 0.78$) (Table I). Not surprisingly, drilling time was shorter when females reused previous oviposition holes (*D. radicum*, $F = 36.75$, $P < 0.0001$; *D. melanogaster*, $F = 24.39$, $P < 0.0001$) (Table I). Probing time spent on parasitized hosts was longer on both host species (*D. radicum*, $F = 14.89$, $P < 0.0001$; *D. melanogaster*, $F = 5.38$, $P = 0.0004$) (Table I). Moreover, on parasitized *D. radicum*, probing time was longer when females reused previous oviposition holes and even longer when they performed an ovicide in addition (Table I). Thus, on both host species, when females reused previous oviposition holes, they saved time during the drilling phase but spent more time during the probing phase. As a result, total handling times of unparasitized and parasitized hosts were similar even if females reused previous oviposition holes and/or performed ovidices (*D. radicum*, $F = 1.19$, $P = 0.31$; *D. melanogaster*, $F = 0.79$, $P = 0.53$) (Table I).

On both host species, rejecting parasitized hosts was the less time-consuming strategy (*D. radicum*, $F = 343.00$, $P < 0.0001$; *D. melanogaster*, $F = 451.15$, $P < 0.0001$) and performing an ovicide before ovipositing did

Table 1. Mean Duration (\pm SE; Seconds) of Initial Exploration, Drilling, Probing, Final Exploration, and Handling of Accepted *D. radicum* and *D. melanogaster* Pupae According to Their Parasitism Status (Unparasitized or Parasitized), the use, or not, of a Previous Oviposition Hole, and the Occurrence of an Ovicide

Host quality	Initial exploration	Drilling	Probing	Final exploration	Handling
<i>D. radicum</i>					
Unparasitized (N = 61)	354 \pm 47 a	237 \pm 13 a	138 \pm 9 a	173 \pm 14 a	904 \pm 58 a
Parasitized					
Without reusing oviposition hole (N = 87)	323 \pm 30 a	226 \pm 11 a	187 \pm 11 b	156 \pm 13 a	893 \pm 36 a
Without reusing oviposition hole + ovidice	218 \pm 38 a	81 \pm 14 b	253 \pm 26 c	214 \pm 61 a	767 \pm 88 a
Reusing oviposition hole (N = 41)	248 \pm 61 a	56 \pm 9 b	328 \pm 39 d	151 \pm 25 a	784 \pm 93 a
Reusing oviposition hole + ovidice (N = 18)					
<i>D. melanogaster</i>					
Unparasitized (N = 64)	205 \pm 16 a	70 \pm 3 a	63 \pm 10 a	60 \pm 11 a	402 \pm 27 a
Parasitized					
Without reusing oviposition hole (N = 45)	201 \pm 18 a	83 \pm 4 b	127 \pm 13 b	46 \pm 6 a	458 \pm 25 a
Without reusing oviposition hole + ovidice (N = 12)	207 \pm 51 a	79 \pm 7 ab	179 \pm 57 b	48 \pm 8 a	514 \pm 73 a
Reusing oviposition hole (N = 20)	195 \pm 63 a	23 \pm 3 c	149 \pm 34 b	62 \pm 13 a	430 \pm 70 a
Reusing oviposition hole + ovidice (N = 14)	233 \pm 97 a	29 \pm 7 c	161 \pm 25 b	44 \pm 5 a	468 \pm 58 a

Note. For each host species, values in the same column followed by different letters are significantly different at $P < 0.05$ (ANOVA).

Table II. Mean Duration (\pm SE; Seconds) of Rejections, Single Ovipositions (With or Without Ovicides), and Double Ovipositions (With or Without Ovicides) on Parasitized *D. radicum* and *D. melanogaster*

Host species	Rejections	Single ovipositions	Single ovipositions + ovicides	Double ovipositions	Double ovipositions + ovicides
<i>D. radicum</i>	65 \pm 7 a (N = 422)	853 \pm 37 b (N = 128)	784 \pm 93 b (N = 18)	1703 \pm 145 c (N = 11)	1217 \pm 140 d (N = 5)
<i>D. melanogaster</i>	39 \pm 3 a (N = 750)	449 \pm 27 b (N = 65)	489 \pm 61 b (N = 26)	—	—

Note. Values in the same line followed by different letters are significantly different at $P < 0.05$ (ANOVA).

not take more time than ovipositing only (Table II). On *D. radicum*, double ovipositions lasted about twice as long as single ovipositions and performing double ovipositions with ovicides even appeared to be faster than performing double oviposition without ovidice (Table II). Handling times were longer on *D. radicum* than on *D. melanogaster* pupae (host rejection, $t = 3.45$, $P = 0.0006$; single oviposition, $t = 7.11$, $P < 0.0001$; single oviposition with ovidice, $t = 2.75$, $P = 0.009$) (Table II).

Offspring Gain of Strategies

On both species, the number of offspring potentially gained per hour from parasitized hosts was higher when females performed ovidices before ovipositing (*D. radicum*, $F = 23.01$, $P < 0.0001$; *D. melanogaster*, $t = 6.18$, $P < 0.0001$) (Table III). On *D. radicum*, double ovipositions provided

Table III. Mean Fitness Gain (\pm SE), in Terms of Offspring Potentially Gained per Hour, Provided by Single Ovipositions (With or Without Ovicides), and Double Ovipositions (With or Without Ovicides) on Parasitized *D. radicum* and *D. melanogaster*

Host species	Single ovipositions	Single ovipositions + ovicides	Double ovipositions	Double ovipositions + ovicides
<i>D. radicum</i>	2.7 \pm 0.1 a (N = 128)	5.7 \pm 0.7 b (N = 18)	1.5 \pm 0.2 c (N = 11)	3.1 \pm 0.3 ac (N = 5)
<i>D. melanogaster</i>	4.9 \pm 0.3 a (N = 65)	9.8 \pm 1.1 b (N = 26)	—	—

Note. Values in the same line followed by different letters are significantly different at $P < 0.05$ (ANOVA for *D. radicum* hosts and t -test for *D. melanogaster* hosts).

a smaller gain, in terms of number of offspring, than single ovipositions, whereas double ovipositions with ovids were equivalent to single ovipositions (Table III). Females potentially gained a greater number of offspring per hour from *D. melanogaster* than from *D. radicum* (single oviposition, $t = 8.80$, $P < 0.0001$; single oviposition with ovid, $t = 2.85$, $P = 0.007$) (Table III).

DISCUSSION

In parasitoid species where females are able to discriminate parasitized hosts from unparasitized ones, females have the choice to accept or reject the parasitized hosts that they encounter. Such decisions are expected to be influenced by patch quality: in particular, the acceptance rate of parasitized hosts should increase when the proportion of such hosts increases in a patch (Strand and Godfray, 1989; van Alphen and Visser, 1990). Our results showed that such was the case in *P. vindemmiae* but that the influence of patch quality on female decisions also depended on host size. Indeed, patch quality influenced the acceptance rate of parasitized hosts in the small species *D. melanogaster* but not in the larger host species *D. radicum*. This indicates that, when confronted with patches of varying quality, generalist parasitoids such as *P. vindemmiae* do not always use the same strategy but, rather, adapt their decisions according to host species and size. Moreover, regardless of the ratio of parasitized hosts, the acceptance rate of parasitized hosts was greater with *D. radicum* than *D. melanogaster* pupae. Discrimination cues might simply be more difficult to find on bigger hosts, leading *P. vindemmiae* females to overevaluate the quality of *D. radicum* patches. Nevertheless, to our knowledge, such difference in discrimination efficiency according to host size has never been shown. Another, more adaptive, explanation would be that females make their decisions regarding parasitized hosts according to other host quality traits such as host species and host size. Indeed, host size is correlated with offspring size in *P. vindemmiae* (Grandgirard *et al.*, 2002).
 Even though host size is not sufficient to discriminate between hosts of different sizes, it is still a useful cue for parasitoids to make their decisions regarding parasitized hosts.

in the oviposition decisions of females (Smith and Fretwell, 1974; Winkler and Wallin, 1987; McGinley and Charnov, 1988; Mayhew, 1998).

Moreover, when females encounter a parasitized host, selfsuperparasitism increases the chances that the winner of the larval competition will be an offspring of the superparasitizing females (Visser *et al.*, 1992). The payoff from this strategy is expected to increase with the intraspecific competition level (i.e., when the number of parasitized hosts increases in the patch) (Visser *et al.*, 1992). Our results showed that this was also the case for *P. vindemmiae*: the occurrence rate of double ovipositions tended to be higher when all hosts were parasitized but this only occurred on *D. radicum* pupae. Double ovipositions were never observed on *D. melanogaster*. As for the acceptance of already parasitized hosts, this difference between species could be due to a more efficient host discrimination on smaller than on larger hosts but also to a bigger investment on fitter hosts.

Our results confirmed the ability of *P. vindemmiae* females to perform ovicides (Nell and van Lenteren, 1982). Ovicide is advantageous since it restores, at least partially, the quality of parasitized hosts (Mayhew, 1997). Moreover, ovicides appear here not to be more costly in terms of host handling time than superparasitism. This may be an intrinsic feature of this strategy: ovicides may be performed only when eggs are found quickly (if not, females could resort to superparasitism). Consequently, ovicide attempts could be more frequent than successful ovicides, but since it is not possible to evaluate potential ovicide attempts, here we only consider successful ones. Thus, it appears that in the two host species tested, the host handling time leading to ovicide with oviposition was similar to the host handling time leading to superparasitism or even to oviposition in unparasitized hosts. Therefore, ovicide appears to be the strategy providing the best fitness gains. As expected, the occurrence of this strategy increased with the proportion of parasitized hosts on *D. melanogaster* (ovicide was performed in about 10% of accepted parasitized hosts in medium-quality patches, whereas it was performed in about 35% of the cases in poor-quality patches). However, this pattern was not found on *D. radicum* (ovicide was performed in about 13% of accepted parasitized hosts whatever the patch quality). Like host acceptance, shifts in this strategy, according to patch quality, also appear to be dependent on host species and size.

In fact, the occurrence rate of ovicides can depend on whether or not they are easy to perform and, in particular, on the difficulty of finding and reaching eggs to pierce (Netting and Hunter, 2000). For *P. vindemmiae*, ovicide is probably more difficult to perform on a large host like *D. radicum* (≈ 6 mm long) than on a smaller host like *D. melanogaster* (≈ 3 mm long), especially when considering that the length of the stylus of the ovipositor is only about 0.75 mm (Goubault, personal observations). This hypothesis is

supported by the fact that females perform ovicides in *D. radicum* pupae only when they reuse the oviposition hole drilled by the first parasitizing females, while on *D. melanogaster*, they can perform ovicides without reusing previous oviposition holes. The location of eggs on the host pupae could also play a role in this difference: eggs can be located anywhere on *D. radicum*, whereas on *D. melanogaster*, eggs are almost always located on the head of pupae (which is the only location in the pupae where there is enough space between the pupa and the puparium for *P. vindemmiae* eggs [Goubault, personal observations]). Ovicide appears to be the fittest strategy on both host species, measured in terms of offspring potentially gained per hour, when unparasitized hosts are scarce. However, ovicides did not exceed 35% of the cases in which parasitized hosts were accepted, even on small *D. melanogaster* hosts, where accessibility to previous eggs seems easy. Consequently, one might ask why *P. vindemmiae* females do not perform ovicides more often. One reason could be that host quality is not completely restored after an ovicide, as was observed in *Laelius pedatus* Say (Hymenoptera: Bethyridae), an ectoparasitoid of dermestid beetle larvae (Mayhew, 1997). In this species, even if offspring survival and development time did not differ between eggs laid on unparasitized hosts and eggs laid on parasitized hosts after an ovicide, offspring from the second type of hosts were slightly smaller. This difference may be explained by the deterioration of the host during the delay between the two ovipositions (Mayhew, 1997). This host-quality restoration issue remains to be tested in *P. vindemmiae*. Another explanation for the low ovicide rate might be related to the risk for a female of killing one of its own eggs: when this risk is high, ovicide should be avoided (Smith and Lessels, 1985). Therefore, ovicide would be advantageous only shortly after females arrive in a new patch (Netting and Hunter, 2000). As females exploit and deplete a patch, the risk of encountering a host already parasitized by themselves increases and the adaptive value of ovicide decreases. Additional experiments would be needed to confirm this hypothesis since in our experiments females never had access to hosts they already parasitized themselves (since these were regularly replaced by hosts of the original quality to keep the patch quality constant).

In generalist parasitoids such as *P. vindemmiae*, conclusions about host selection decisions according to the proportion of parasitized hosts in a patch may not be systematically transposable to host species other than the one being tested. However, our results show that female parasitoids are able to adapt their oviposition decision rules according to multiple patch-quality components that interact. In particular, shifts between host selection strategies according to the ratio of parasitized hosts depend on host species and size. On the other hand, up to now, ovicide has often been underestimated, probably because of the difficulty of studying it. Nevertheless, our results

show that ovicide is a possible host selection strategy that has to be taken into account.

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