Intraspecific Variations in Host Discrimination Behavior in the Pupal Parasitoid *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae)

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ABSTRACT   In solitary parasitoid species, superparasitism incurs a high cost because only one individual can emerge per host. While avoiding already-parasitized hosts seems advantageous, it requires an ability to discriminate between parasitized and unparasitized hosts. The ability to discriminate can be based on physical or chemical cues or signal associated either internally or externally with a given host. The type of stimuli used to recognize parasitized hosts generally depends on the features of these hosts but also on costs and benefits associated with reusing them. Some local factors such as mortality rate of females, host availability, and competition level can influence this trade-off. In species that occupy a large geographic range, local conditions may favor either external or internal mechanisms of host discrimination. We describe the behaviors associated with host discrimination in *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae), a solitary pupal parasitoid of cyclorraphous dipteran species. To detect potential intraspecific variability in their host discrimination behavior, we compared two *P. vindemmiae* populations originating from different geographical areas in France. Our results revealed different host discrimination strategies in both populations and indicated a potential trade-off between the speed and the accuracy of host discrimination. One population discriminated hosts externally (faster but less accurately), whereas the other discriminated internally (more slowly but more accurately). In our experimental conditions, these two strategies resulted in differences in the fitness gains of both populations. The ecological conditions that could have selected for such differences in the host discrimination and oviposition strategies of the two populations remain to be investigated.

KEY WORDS   host quality, behavior, external/internal marking, superparasitism

THE PROCESS OF HOST selection is a central step in the reproductive biology of parasitoid insects. Optimal Foraging Theory predicts that females will maximize their lifetime fitness by optimizing the time and energy invested in evaluating the quality of their hosts (Stephens and Krebs 1986). The quality of a host may depend on its species, developmental stage, size, and whether it was previously parasitized (van Alphen and Vet 1986). Whereas predators remove prey items from the habitat, parasitized hosts often remain in place and can be encountered again by parasitoid females. Parasitism status is thus a key component of host quality, especially in solitary parasitoids where only one parasitoid can develop per host. Because superparasitism by solitary species is often associated with a high fitness cost (van Lenteren 1981), the ability to distinguish parasitized from unparasitized hosts, called host

discrimination (van Alphen and Nell 1982), is expected to be advantageous. Numerous studies have focused on host discrimination and showed that it is usually based on several physical or chemical signals (i.e., stimuli presumed to have evolved to convey information from a sender to a receiver) or cues (i.e., products of selection on a trait other than communication that convey information only incidentally) (Nufio and Papaj 2001), located either inside or outside the hosts (van Alphen and Visser 1990, Godfray 1994, Nufio and Papaj 2001).

The types of stimuli involved in the recognition of parasitized hosts are partially constrained by host features, such as developmental stage, mobility, accessibility, or their ability to defend themselves. For example, marking the host externally seems to be common among egg parasitoids but not among parasitoids attacking other stages of the host (Bosque and Rabinovich 1979). Indeed, especially in koinobiont parasitoid species, larval hosts continue their development, and external marks risk being lost when the cuticle is shed. Moreover, larvae and pupae are generally less accessible than eggs to antennal examina-

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tion. Concealed parasitized hosts are expected to be recognized on the basis of internal stimuli (Bosque and Rabinovich 1979) even if they can also be recognized in certain species through marks left on the patch (Hoffmeister and Roitberg 1997).

The use of external or internal marking is also influenced by their relative benefits: external discrimination could be more advantageous than internal discrimination because they are detected faster as the time required for host drilling is saved (van Baaren et al. 1995), but external cues may be less reliable because, in certain cases, they persist for only a short period of time (Chow and Mackauer 1986). Although long-lived external marks are used by some parasitoids (Höller et al. 1991), external marks tend to be short-lived (Godfray 1994) because they are generally water soluble (Okuda and Yeargan 1988, Godfray 1994) and easily degraded (Harrison et al. 1985). The period of efficacy of a mark depends on the pay-off of reusing a host (Roitberg and Mangel 1988, van Alphen and Visser 1990). Thus, the use of more or less long-lived and potent marks should be selected for, depending on the probability of re-encountering hosts and the probability that a second clutch will survive on a parasitized host (Messina et al. 1991).

In species whose distribution range covers a variety of habitats, factors influencing these probabilities may differ from a population to another. Therefore, inter-population variability may be expected on the type of stimuli involved in host discrimination (Messina et al. 1991), and consequently, different behavioral mechanisms associated with host discrimination may be selected in different populations. In particular, variation in host discrimination behavior could be present if some local factors, such as mortality rate, intraspecific competition level, or host distribution, influence the probability of encountering parasitized hosts and the costs and benefits of reusing such parasitized hosts.

We studied the host discrimination behavior of *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae), a cosmopolitan solitary ectoparasitoid attacking pupae of a range of cyclorrhaphous dipteran species such as *Drosophila melanogaster* Meigen, *Ceratitis capitata* Weidemann, *Rhagoletis* sp., *Delia radicum* L. (*Hylemia brassicae* Bouché), *Fannia canicularis* L., and *Musca domestica* L. (Rueda and Axtel 1985). *P. vindemmiae* is considered a good candidate for the biological control of flies associated with poultry and livestock manure in Brittany. Females of this parasitoid are able to discriminate parasitized from unparasitized hosts (Nell and van Lenteren 1982). The oviposition sequence of *P. vindemmiae* females is as follows (C. Billet, unpublished data): after antennal contact of the host, females explore its surface with the tip of their abdomen, drill a hole in the puparium, and insert their ovipositor into the puparium. After laying an egg, they withdraw their ovipositor from the puparium, search the hole with the tip of their abdomen, and cover it with a transparent and viscous secretion. However, the mechanism of host discrimination of *P. vindemmiae* is still unknown. Females could assess the parasitism status of their hosts either externally, by

detecting the female secretion (as observed in many other parasitoid species: e.g., Rabb and Bradley 1970, Bosque and Rabinovich 1979, Strand and Vinson 1983, Conti et al. 1997, Sadoyama 1998), or they could assess it internally, by detecting with their ovipositor cues located inside the puparium, such as the presence of conspecific eggs or changes in host hemolymph (Strand 1986).

In this study, we searched for inter-population variability in the host discrimination behavior of this parasitoid by comparing two populations originating from different geographical areas in France. One population originated from the Lyon area in southeastern France, whereas the other came from the Rennes area in northwestern France (Brittany). These two regions differ in their climates and host abundance, so their *P. vindemmiae* populations are likely to be submitted to different selection pressures. To compare the host discrimination strategies of these two populations, we described the behaviors associated with host discrimination. We also estimated the mean fitness gain of females from both populations under our experimental conditions.

Materials and Methods

Rearing

The host, *D. radicum*, originated from pupae collected from cabbage fields (Le Rheu, Brittany, France) in 1994. The flies were reared on rutabaga roots (*Brassica napus* L.) at $20 \pm 2°C$, $60 \pm 10\%$ RH, and 16L:8D, according to the technique described in Neveu et al. (1996). Preliminary experiments showed *P. vindemmiae* tended to oviposit more readily into *D. radicum* pupae that were 5–10 d old (Grandgirard et al. 2002). In all our experiments, we used 7- to 9-d-old pupae.

Two populations of *P. vindemmiae* were collected in two different geographical areas: one near Lyon, France (45°46 N, 4°50 E) in 1996 and the other near Rennes, France (48°06 N, 1°20 W) in 2000. Both populations were reared on pupae of *D. radicum* at $25 \pm 1°C$, $60 \pm 10\%$ RH, and 16L:8D. Adults were maintained in petri dishes ($\emptyset = 8.5$ cm; h = 2.7 cm) and supplied with honey, water, and ≈200 host pupae that were replaced three times a week. Parasitized pupae were stored in petri dishes under the same conditions until the emergence of new adults.

Experimental Procedures

The *P. vindemmiae* females used in all experiments were 24 h old and were fed with honey. To have females mated and experienced, they were individually placed, before 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 1–4 h. By dissection of pupae, we found that 90% of the females submitted to such conditions had at least one oviposition experience. All experiments were performed at $22 \pm 1°C$ and $40 \pm 10\%$ RH.

Three categories of 7- to 9-d-old *D. radicum* pupae, ≈6 mm long, were used as hosts in all tests: unparasitized hosts, parasitized hosts with female secretion (i.e., pupae that received a parasitoid egg and where the female was observed depositing a secretion after oviposition), and parasitized hosts without female secretion (i.e., immediately after oviposition, females were separated from pupae by being delicately pushed with a thin brush to prevent the females from depositing any post-oviposition secretion). Parasitized hosts with or without female secretion were obtained by allowing conspecific females to lay one egg per pupa 0–6 h before the beginning of the experiments. The behavior of secretion deposition is similar in the two populations.

Host Discrimination Behaviors

To determine how females of both populations discriminate hosts, we examined the behavior of females that were offered two different types of hosts. Females of both populations were tested separately. Two experiments were performed.

Experiment 1. Each female was presented with five unparasitized hosts and five parasitized hosts with female secretion ($N = 30$ Lyon-population females and $N = 27$ Rennes-population females).

Experiment 2. Each female was presented with five parasitized hosts with female secretion and five parasitized hosts without female secretion ($N = 15$ Lyon-population females and $N = 28$ Rennes-population females).

In both experiments, females were placed individually in petri dishes ($\varnothing = 8.5$ cm; h = 2.7 cm). The position of each host type was alternated in the petri dish so that females had the same probability of encountering both types. Hosts drilled during the experiments were immediately replaced by hosts of the same type to keep the patch quality constant, whereas hosts touched by the antennae of the females were not replaced so that females were not disturbed too much. 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 activities were recorded for 2 h: encounter with pupae, antennal rejection, abdominal rejection (after the antennal exploration, females continue to examine the host externally by tapping on its surface with the tip of their ovipositor sheath [third valvulae], generally called the tip of the abdomen), sting rejection, and oviposition. Oviposition was distinguished from sting (i.e., insertion of the ovipositor without oviposition) by the typical abdominal contractions that occur only when an egg is deposited (C. Billet, unpublished data).

The numbers of encounters with the different types of hosts were compared with generalized linear models assuming a Poisson error using GLIM 3.77 (McCullagh and Nelder 1989). The frequencies of each activity (i.e., different types of rejection or oviposition) on the different types of hosts were compared with a paired *t*-test performed after arcsine square-root transformation. These tests were only carried out within populations. We did not carry out additional statistical analysis between populations because tests done within populations gave highly significant results. It has to be noted that the frequency of antennal rejections of hosts could have been artificially increased because hosts were replaced only when they were drilled. To estimate differences in the duration of discrimination behaviors between populations, we recorded the amount of time it took for females of both populations to reject a host after externally and internally assessing a given host (i.e., abdominal and sting rejections). These durations were compared between populations with *t*-tests.

Mean Fitness Gain (Experiment 1)

In experiment 1, we also compared the acceptance frequency of parasitized hosts and the oviposition rate (i.e., number of eggs laid per 2 h) of both populations with a *t*-test. The mean fitness gain obtained by females of each population during the experiment was calculated by allocating a gain of one for each oviposition in an unparasitized host (the mortality rate is negligible) and a gain of 0.5 in a parasitized host as a second egg laid within 6 h after the first one has a survival probability of 0.5 (Goubault et al. 2003). The comparison of mean fitness gain of both populations was performed with a *t*-test.

Results

Host Discrimination Behaviors

Experiment 1: Unparasitized Hosts Versus Parasitized Hosts with Female Secretion. The mean number of unparasitized and parasitized hosts encountered did not differ significantly in both populations (Lyon-population: 8.30 ± 6.62 unparasitized hosts and 8.47 ± 6.74 parasitized hosts; $\chi^2 = 0.07$, 1 df, $P > 0.05$; Rennes-population: 6.41 ± 5.80 unparasitized hosts versus 7.33 ± 5.74 parasitized hosts; $\chi^2 = 1.69$, 1 df, $P > 0.05$). Within both populations, there was no significant difference in the frequency of rejection of unparasitized versus parasitized hosts after antennal examination (Lyon-population: Fig. 1A, $t = 0.77$, 29 df, $P = 0.45$; Rennes-population: Fig. 1B, $t = 1.73$, 26 df, $P = 0.10$). However, the rate of rejection of unparasitized versus parasitized hosts after abdominal examination differed significantly in the Rennes-population (Fig. 1B, $t = 5.62$, 26 df, $P < 0.0001$) but not in the Lyon-population (Fig. 1A, $t = 0.59$, 29 df, $P = 0.56$). The reverse was found for the rate of sting rejection that differed significantly in the Lyon-population (Fig. 1A, $t = 3.04$, 29 df, $P = 0.005$) but not in the Rennes-population (Fig. 1B, $t = 0.88$, 26 df, $P = 0.39$). On average, both populations oviposited significantly more in unparasitized than parasitized hosts (Lyon-population: Fig. 1A, $t = 2.60$, 29 df, $P = 0.02$; Rennes-population: Fig. 1B, $t = 4.83$, 26 df, $P < 0.0001$). Thus, although females of both populations preferred laying their eggs on unparasit-

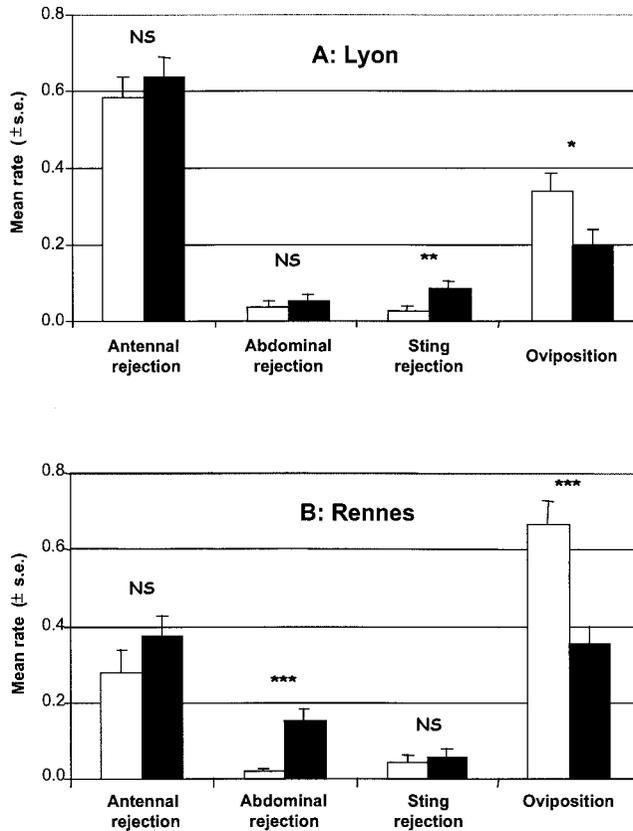**Fig. 1.** Mean rate ± SE of antennal rejections, abdominal rejections, sting rejections, and ovipositions on unparasitized *D. radicum* pupae (white columns) and parasitized pupae with female secretion (black columns) by *P. vindemmiae* females of the Lyon-population (A) and the Rennes-population (B). NS, nonsignificant difference; *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$.

ized hosts, the Lyon-population females rejected parasitized hosts after stinging, whereas the Rennes-population females rejected parasitized hosts after abdominal exploration.

Experiment 2: Parasitized Hosts with Versus Without Female Secretion. In both populations, there was no difference in the number of parasitized hosts with and without secretions that females encountered (Lyon-population: 12.93 ± 13.15 parasitized hosts with female secretion versus 11.20 ± 10.83 parasitized hosts without female secretion, $\chi^2 = 1.59$, 1 df, $P > 0.05$; Rennes-population: 7.50 ± 5.35 parasitized hosts with female secretion versus 7.79 ± 5.20 parasitized hosts without female secretion, $\chi^2 = 0.15$, 1 df, $P > 0.05$). None of the recorded behaviors were modified by the presence of the female secretion on the pupa in both populations (comparison of the frequency of the different activities realized on parasitized hosts with versus without secretion: Lyon-population: Fig. 2A, antennal rejection: $t = 0.12$, 12 df, $P = 0.90$; abdominal rejection: $t = 0.66$, 12 df, $P = 0.52$; sting rejection: $t = 0.02$, 12 df, $P = 0.99$; oviposition: $t = 0.33$, 12 df, $P = 0.74$; Rennes-population: Fig. 2B, antennal rejection: $t = 1.11$, 27 df, $P = 0.28$; abdominal rejection: $t = 1.19$,

27 df, $P = 0.25$; sting rejection: $t = 0.48$, 27 df, $P = 0.63$; oviposition: $t = 0.56$, 27 df, $P = 0.58$).

The Lyon-population females discriminated between parasitized and unparasitized hosts after probing the puparium, whereas the Rennes-population females discriminated after external examination of a host puparium. External rejections were faster than internal rejections because females did not drill the puparium (Lyon-population: external rejections = 113.34 ± 17.24 s [$N = 23$], internal rejections = 991.36 ± 156.70 s [$N = 26$], $t = 5.24$, 47 df, $P < 0.0001$; Rennes-population: external rejections = 134.99 ± 15.65 s [$N = 28$], internal rejections = 604.08 ± 88.05 s [$N = 17$], $t = 6.61$, 43 df, $P < 0.0001$). The durations of external and internal rejections were similar in both populations (external rejections: $t = 0.93$, 49 df, $P = 0.36$; internal rejections: $t = 1.87$, 41 df, $P = 0.07$).

Mean Fitness Gain (Experiment 1)

Females from the Lyon-population accepted parasitized hosts less frequently than females of the Rennes-population (acceptance of parasitized hosts, Lyon-population: $19.37 \pm 4.42\%$; Rennes-population:
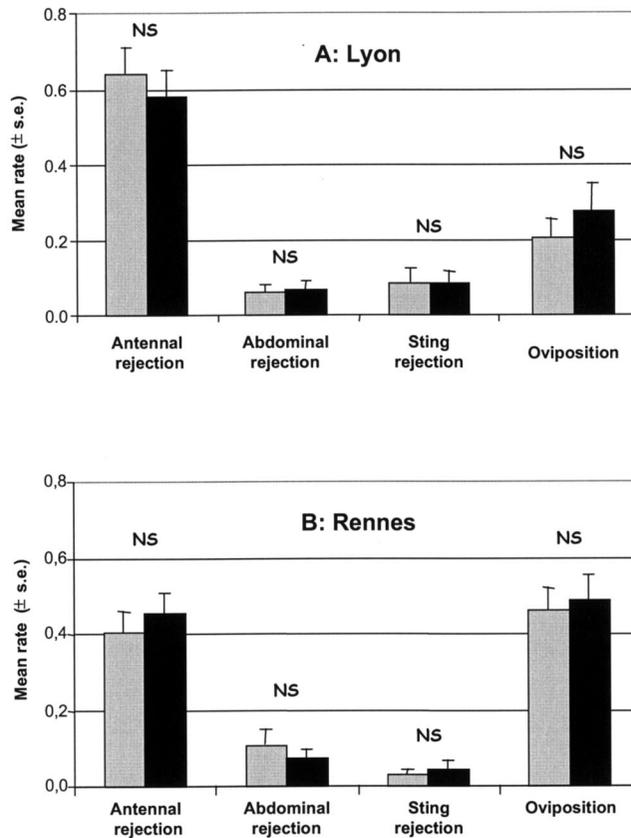
Fig. 2. Mean rate ± SE of antennal rejections, abdominal rejections, sting rejections, and ovipositions on parasitized *D. radicum* pupae with female secretion (black columns) and parasitized pupae without female secretion (gray columns) by *P. vindemmiae* females of the Lyon-population (A) and the Rennes-population (B). NS, nonsignificant difference.

35.63 ± 4.45%; $t = 2.94$, 55 df, $P = 0.005$). In addition, the Lyon-population females parasitized fewer hosts during the experiment (on average 2.83 ± 0.32 hosts parasitized per female per 2 h) than the Rennes-population females (on average 5.30 ± 0.28 hosts parasitized per female per 2 h; $t = 5.83$; 55 df; $P < 0.0001$). During the experiment, Lyon-population females had a significantly lower fitness gain than Rennes-population females (mean fitness gain, Lyon-population females: 2.35 ± 1.50 progeny per 2 h; Rennes-population females: 4.13 ± 1.21 progeny per 2 h; $t = 4.90$, 55 df, $P < 0.0001$).

Discussion

An apparently easily detectable stimulus is available to *P. vindemmiae* females to discriminate parasitized from unparasitized hosts: the secretion that females deposit on hosts after oviposition. Nevertheless, in both populations, the implication of this secretion in host discrimination could not be shown because host selection behavior was not modified by its presence. This is surprising because female secretions have been linked to host discrimination in other parasitoid species (Godfray 1994). Indeed, when such mark deposition by females has been described, these substances

have been shown to be involved in host discrimination (Rabb and Bradley 1970, Bosque and Rabinovich 1979, Strand and Vinson 1983, Conti et al. 1997, Sadoyama 1998).

Because host discrimination was confirmed by our study, the *P. vindemmiae* females from both populations were able to assess the parasitism status of hosts on the basis of other stimuli that remain to be identified. However, females from both populations did not use the same types of stimuli, and these stimuli were detected at different stages of their oviposition sequence. Lyon-population females discriminated hosts on the basis of stimuli internal to the host puparium because they rejected parasitized hosts only after probing through the puparium (i.e., sting rejection). Rennes-population females discriminated on the basis of external cues they perceived while exploring the host surface by tapping with the tip of their ovipositor sheath (i.e., abdominal rejection). To our knowledge, this is the first time that two parasitoid populations are shown to differ in their host discrimination behavior. Other studies showed inter-population variability in host discrimination, but they did not identify behavioral variations in the way parasitized hosts were recognized (in parasitoids: Marris et al.

1996, van Baaren and Boivin 1998a; in phytophagous insects: Messina et al. 1991).

The existence of plasticity in host discrimination behavior has been shown in some parasitoid species (van Lenteren 1976, Hofsvang 1988, van Baaren and Boivin 1998b). Like *P. vindemmiae*, the females of *A. victus*, for example, can also reject parasitized hosts either after antennal exploration (antennal rejection) or after the insertion of their ovipositor (sting rejection) (van Baaren et al. 1995). By learning to associate the presence of the external pheromone with the presence of the internal one, *A. victus* females are able to adapt to different environmental conditions (van Baaren and Boivin 1998b). However, in *P. vindemmiae*, plasticity does not seem able to explain the behavioral difference found between the two populations. Indeed, plasticity would have resulted in females of both populations switching to the optimal behavior under our experimental procedures, and thus, discriminating in the same manner. Instead, the behavioral difference we find suggests that each population has evolved its own optimal host discrimination behavior in response to local selective pressures, resulting in a genetic difference persisting despite several generations of rearing the two strains in identical conditions in the laboratory.

External discrimination seems more advantageous than internal discrimination because it allows an easier and faster host quality evaluation (van Baaren et al. 1995). However, external cues or signals can be less reliable than internal ones, especially if external stimuli are rapidly degraded (Harrison et al. 1985, Okuda and Yeargan 1988, Godfray 1994). Therefore, in some cases, there can be a trade-off between host discrimination speed and its accuracy, as proposed by Glaizot and Arditi (1998). These authors developed an Optimal Inspection Time model that predicts that the longer a parasitized host is inspected, the higher the probability that it will be recognized as parasitized and therefore rejected. Consequently, two strategies can be selected, either a quick evaluation with the associated risk of making a wrong decision or a longer but more precise evaluation. Our results might illustrate the existence of these two strategies. Rennes-population females, which discriminate hosts externally, rejected parasitized hosts 7.5 times faster on average than Lyon-population females, which discriminate hosts internally (the time difference is mainly because of the drilling of a hole in the puparium). However, external discrimination would also seem to be less accurate because the percentage of already-parasitized hosts accepted by Rennes-population females was ≈36 ± 4% compared with 19 ± 4% in Lyon-population females using internal discrimination. An alternative hypothesis would be that the populations discriminate with similar accuracies, but the pay-off of superparasitism is higher in the Rennes area so that the Rennes strain has been selected to accept parasitized hosts more readily. The Rennes-population females seemed to adopt a time-limited strategy: they discriminated quickly, accepted parasitized hosts more often, and as a result, laid more eggs per time unit. In con-trast, the Lyon-population females seemed to adopt an egg-limited strategy: they took more time to discriminate and thus laid fewer eggs, but used better quality hosts on average. The presence of different strategies concerning time and egg limitation is reflected in differences in female egg loads between populations: Rennes-population females have a larger egg load (17.77 ± 0.34 eggs) than Lyon-population females (12.93 ± 0.47 eggs; $t = 8.41$, 58 df, $P < 0.0001$). To estimate the fitness gain of these two strategies in *P. vindemmiae*, the number of offspring potentially gained by the females tested during the experiment was calculated in relation to the potential survival of each egg laid (Goubault et al. 2003). Despite the lower average quality of the hosts parasitized by the Rennes-population, its strategy seemed superior under our experimental conditions.

Although the two strains were not maintained in the laboratory for the same amount of time, we feel that the differences we observed are more linked to their area of origin than to their rearing. Indeed, the host discrimination behavior of the Lyon-population females was tested on three successive occasions (shortly after being put in colony, 1 yr later, and for this experiment), and it did not change. Which ecological constraints could have selected for such differences in the host discrimination behavior and oviposition strategies of the two populations remains to be investigated. In fact, any factor that plays on the trade-off between host evaluation accuracy and host evaluation speed could influence such a variation. For example, the intraspecific competition level could have played an important role because, in a high competition situation, it is more advantageous to be faster (i.e., by discriminating externally for example) to oviposit more than conspecifics even if it means being less selective (van Dijken and van Alphen 1991). Other differences between areas of origin such as host abundance, host searching time, and size of available hosts could also influence the discrimination strategies of parasitoid populations. Indeed, current studies with the Rennes-population (Goubault et al. 2004) show that host species and size (*D. radicum* versus *D. melanogaster*) greatly influence the host selection strategy of parasitized hosts in *P. vindemmiae*. The Lyon and Rennes areas differ in climate and agricultural productions; therefore, the availability of the different host species potentially attacked by a generalist parasitoid such as *P. vindemmiae* may vary greatly between these two areas. Small-sized fruits flies like *D. melanogaster*, *C. capitata*, and *Rhagoletis* sp. are especially abundant in southeastern France (i.e., Lyon area) where orchards and vineyards are the prevalent crops. On the contrary, large-sized dipteran species like *M. domestica* and other manure flies are very frequent and can even be a real nuisance locally in northwestern France (Brittany), because this region specializes in dairy farming and intensive poultry and pig production.

We hope to be able to conduct field studies linking the actual ecological constraints met by *P. vindemmiae* populations depending on their areas of origin and

their reproduction strategies in the future. Besides its ecological significance, such knowledge would be very relevant for the biological control of manure flies, because the area of origin of the biocontrol agents could strongly affect their efficiency.

Acknowledgments

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