

INTRODUCTION

Invading species encounter novel environments, both biotic and abiotic. Whether an invader is successful can depend on its interactions with native species. Parasitoids and predators may play a role here: invaders may have increased chance of success if local parasitoids and predators either do not attack them or are simply less successful against them than against native species, with which they have been co-adapting for some time.

Parasitoid wasps often attack *Drosophila* larvae (Fleury *et al.*, 2009) by laying an egg on fly larvae. After hatching, larval parasitoids burrow into the larval fly. Some fly species (e.g. *D. melanogaster*) then mount a cellular immune response ('encapsulation') that is sometimes successful and kills the parasitoid (see Nappi *et al.*, 2009), whereas other species (e.g. *D. subobscura*) cannot mount a successful immune response (Eslin and Doury, 2006; Havard *et al.*, 2009) and so are inevitably killed by the parasitoid larva, which usually metamorphoses into an adult wasp.

Rates of parasitism on *Drosophila* in nature are generally high. In fact, up to 80% of *Drosophila* larvae on a given fruit can be parasitized (see Fleury *et al.*, 2009). Consequently, parasitoids can cause major mortality in fly populations (Parsons, 1977; Janssen *et al.*, 1988; Driessen *et al.*, 1990; Boulétreau *et al.*, 1991; Fleury *et al.*, 2004) and thus play a role in the success (or lack thereof) of invasions. Because one of the two 'partners' in this co-evolutionary interaction always dies, selection pressures on both are strong, especially in flies that have an immune response.

Host–parasitoid systems involving frugivorous *Drosophila* communities have been widely studied in Europe (Janssen *et al.*, 1988; Hardy and Godfray, 1990; Allemand *et al.*, 1999; Fleury *et al.*, 2004, 2009). In Igé (Burgundy, central east France), for example, three host species of flies (*D. melanogaster*, *D. immigrans*, *D. subobscura*) dominate the frugivorous *Drosophila* community. Parasitoids are represented primarily by *Leptopilina heterotoma* (Figitidae) and to a lesser extent by *Asobara tabida* (Braconidae) (Fleury *et al.*, 2009).

Host–parasitoid communities involving *Drosophila* are less well studied in North America than in Europe. Fortunately, however, many of the same species found in Igé can be found in some North American sites. For example, both *A. tabida* (Hoang, 2002) and *L. heterotoma* occur near Seattle in the Pacific Northwest (Washington State, USA). How long these parasitoids have been on the American continent is unknown but is apparently recent (Carton *et al.*, 1986). *Leptopilina heterotoma* was first reported in the USA (east coast) by Nordlander (1980), and *A. tabida* was first reported in North America by Hoang (2002). And the same three species of *Drosophila* found in Igé are also found in the Pacific Northwest, where all are invasive, presumably from the Old World (Beckenbach and Prevosti, 1986; Pascual *et al.*, 2007).

Drosophila subobscura offers an opportunity to study host–parasitoid relationships in an invasive species. This *obscura*-group fly is native to the Old World but invaded Chile in the late 1970s (Brncic *et al.*, 1981). It soon jumped to North America and spread rapidly along the west coasts of both continents (Beckenbach and Prevosti, 1986; Pascual *et al.*, 2007). Despite having to compete with native *obscura*-group flies in North America, *D. subobscura* soon became the most common fly collected at many localities in the Pacific Northwest (Beckenbach and Prevosti, 1986; Huey and Pascual, 2009). Whether its success in a new environment is the result of partial escape from Old World parasitoids [e.g. *Asobara tabida*, *Leptopilina heterotoma* (Fleury *et al.*, 2009)] is an open and largely unstudied issue. It does face some parasitoids in the New World: *Asobara tabida* is present in the Pacific Northwest and successfully parasitizes local

D. subobscura, as least in the laboratory (Hoang, 2002). However, before the present study, *L. heterotoma* had never been found in the Pacific Northwest, although it had been collected in central California (Schlenke *et al.*, 2007). This pattern suggested to us *a priori* that the success of *D. subobscura* in the Pacific Northwest (Huey and Pascual, 2009) might in part be due to a relatively depauperate (at least in terms of number of species) parasitoid fauna in this area.

To study interactions between *D. subobscura* and its parasitoids in the Old and New Worlds, we collected hosts and parasitoids in Igé (France) and near Seattle (USA). We soon discovered that *L. heterotoma* was in fact present [along with *A. tabida* (Hoang, 2002)] in Seattle: thus the local parasitoid fauna is not in fact depauperate as expected. Nevertheless, this discovery presented an opportunity to evaluate local adaptation of hosts and parasitoids. Consequently, we reared the two species together in all possible combinations (2 hosts $\times$ 2 parasitoids, factorial design) in the laboratory. Local adaptation of *L. heterotoma* would be evident if wasps from Seattle were more successful on *D. subobscura* from Seattle than on *D. subobscura* from Igé, and vice versa. Similarly, we wished to determine whether *D. subobscura* from the New World was relatively well defended against local *L. heterotoma*, as might be expected if ‘partial escape from parasitism’ is involved in the success of *D. subobscura* in this area.

MATERIALS AND METHODS

Traps with banana baits were placed in shade in a forested habitat in Woodinville, WA (47.79°N, 122.07°W, approximately 27 km northeast of Seattle, WA) in mid-June 2007 (hereafter ‘Seattle’ flies). After 2 weeks in the field, traps were retrieved and shipped by air to the laboratory in Lyon. *Drosophila* and parasitoids that emerged were initially identified morphologically and then confirmed molecularly [CytB for *D. subobscura* (Gao *et al.*, 2007); ITS2 for *L. heterotoma* (Allemand *et al.*, 2002)]. Two species of *Drosophila* (*D. immigrans*, *D. subobscura*) and two species of parasitoids (*A. tabida*, *L. heterotoma*) emerged from this collection.

Traps were similarly placed in a mixed-fruit orchard in Igé (Burgundy, France, 46.39°N, 4.74°E) for 2 weeks in early April 2007 and directly transferred to Lyon. Only *D. subobscura* and *L. heterotoma* emerged. Because only *D. subobscura* and *L. heterotoma* were found in both Seattle and Igé collections, we restricted experiments to these two species.

Strains of *D. subobscura* and of *L. heterotoma* were founded from about 30 females from each locality. *Drosophila* were mass reared at 22°C, fed artificial diet (David and Clavel, 1965), and maintained on a 12/12 h light/dark photoperiod. Before testing, *L. heterotoma* strains were mass reared on *D. melanogaster* for three generations and then for six generations on *D. subobscura* (maintained as above).

All experiments were run simultaneously in spring 2008. We used a factorial experimental design in which *L. heterotoma* from Igé or from Seattle were reared on *D. subobscura* from Igé or from Seattle (giving four treatments). Experimental protocols followed Boulétreau and Fouillet (1982). For each treatment, we first set up 20 vials with 100 host eggs at 22°C (12/12 h light/dark). After 24 h (to allow eggs to hatch), we added one female wasp to each vial for 24 h. We then transferred each female to a new vial (as above) for another 24-h exposure. Vials were maintained until flies and wasps had eclosed.

To assess the quality of the development of *D. subobscura* from Seattle and from Igé in the absence of parasitoids (control vials), we seeded five control vials per population with 100 *Drosophila* eggs for two consecutive days (as above, but without parasitoids). This

provides an estimate of the expected number of flies (T) when parasitoids are absent. (*Note:* T is the average number of flies emerging from control vials.)

We also seeded 20 vials each with 100 fly eggs and a parasitoid, as described above. Then we counted the total numbers of *Drosophila* (d_i) and of parasitoids (p_i) emerging from the two vials for each female parasitoid.

Following Boulétreau and Fouillet (1982), we scored two indices that summarize host–parasitoid interactions. First, ‘degree of infestation’ (DI) measures the proportion of host larvae that were successfully parasitized and is estimated as $(T - d_i)/T$. (Recall that *D. subobscura* do not survive parasitoid attack.) Thus a high DI indicates that a parasitoid took a heavy toll on the flies. Second, ‘success rate of parasitism’ (SP) measures the probability that an infested larva gives rise to an adult wasp (Boulétreau and Fouillet, 1982) and is estimated as $p_i/(T - d_i)$. In some cases, $p_i > (T - d_i)$; for these we set $SP = 1$.

Another way to judge the effect of a host on parasitoids is to measure aspects of the fitness of emerging adult parasitoids. Consequently, we measured potential fecundity and size of parasitoids.

To estimate potential fecundity, we maintained newly emerged females for 5 days (honey, no access to hosts) to allow their oocytes to mature fully. Then we dissected each female and counted the number of oocytes in one of her ovaries. [*Note:* An individual’s total fecundity, which is approximately twice the number of eggs contained in one ovary, is a reliable estimate of her reproductive potential (Eijls and Van Alphen, 1999).] For each combination of host and parasitoid, we measured the fecundity of five females taken haphazardly from each of 10 vials (thus 50 females per combination).

To index the body size of parasitoid adults, we measured the length of the tibia of the right back leg of each female (above). In a separate experiment, we measured three wing lengths on each of 30 female *Drosophila* from Igé and Seattle and then computed principal component loadings (‘prcomp’ in R version 2.7.0).

In 27 of 80 vials, no *Drosophila* larvae were parasitized, and we excluded these vials from analysis. For the two indices (SP and DI), data were arcsine square-root transformed and then analysed using a linear model; but we report untransformed averages.

For size and fecundity of *Leptopilina*, we used a mixed-model approach, with *Drosophila* and *Leptopilina* sources as fixed effects, and vial as a random effect. For fecundity, we used a Poisson error distribution; and for size, we assumed a Gaussian error. Fecundity and size were measured on the same individuals because the number of eggs can be correlated with size (Eijls and van Alphen, 1999).

RESULTS

‘Success rate of parasitism’ approximates the probability that an infested *Drosophila* larva gives rise to an adult wasp and thus indicates the success of parasitism. *Leptopilina* success rate was high and very similar in all treatments (range 0.83–0.86). Not surprisingly, SP was independent of the source population of the fly ($P = 0.661$), of the wasp ($P = 0.536$), and also of their interaction ($P = 0.364$).

‘Degree of infestation’ measures the impact of parasitoids on flies. Specifically, it is the proportional reduction in the expected number of flies that emerge when a parasitoid was present in the vial. Degree of infestation was independent of the source population of *Drosophila* and of *Leptopilina*, but was significantly affected by their interaction (Fig. 1A). Specifically, *Leptopilina* from Seattle exert a higher DI on *Drosophila* from Seattle than on

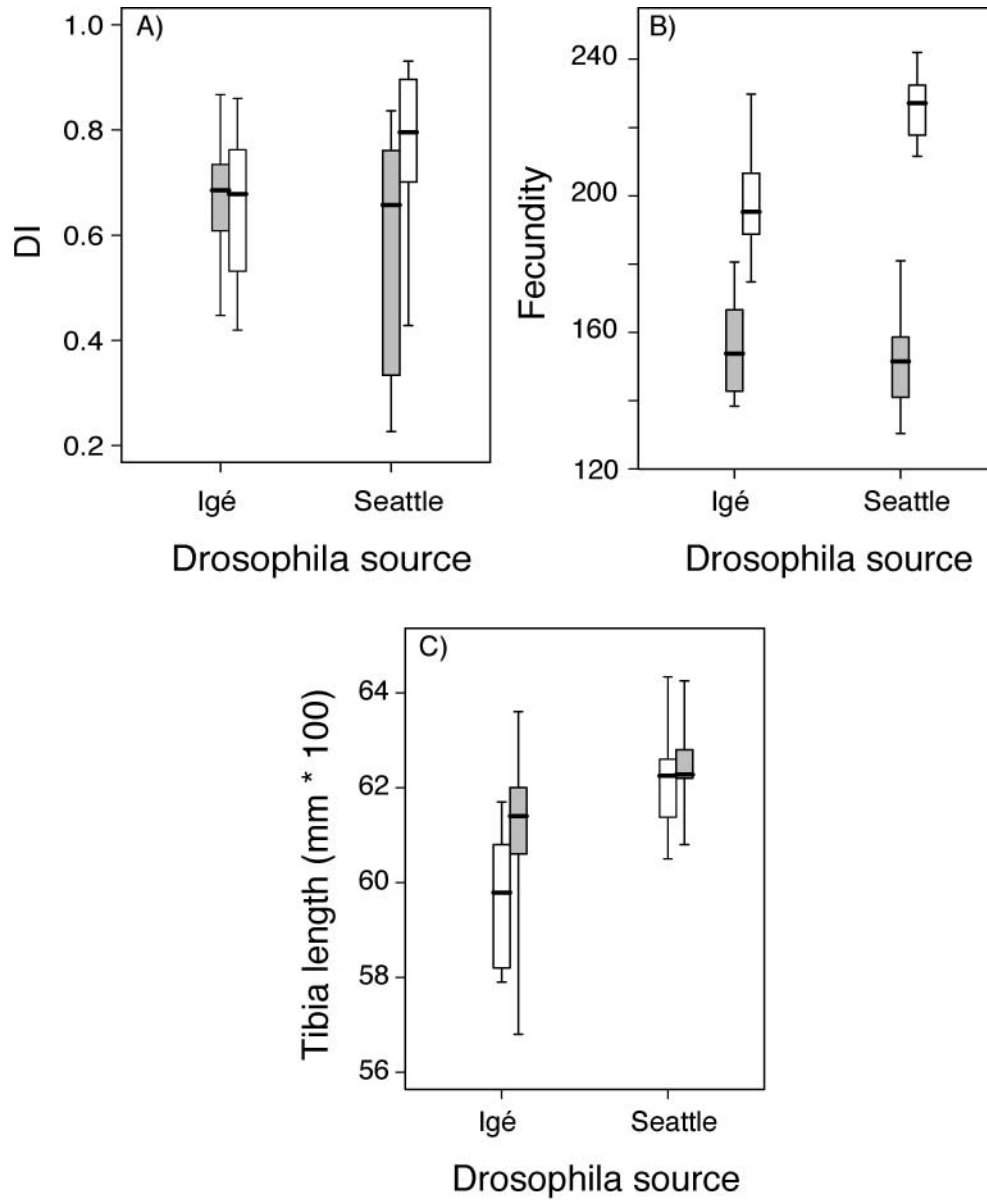


Fig. 1. (A) Box plots of DI for different populations of hosts (*Drosophila*, x-axis) and parasitoids (*Leptopilina*). Vertical lines delimit the range, boxes delimit the interquartile range, and horizontal line is the median. Grey boxes are for *Leptopilina* from Igé, and white boxes are for Seattle. (B) Box plots of fecundity. (C) Box plots of tibia length (mm*100).

those from Igé. Similarly, *Leptopilina* from Igé have a greater impact on *Drosophila* from Igé than from Seattle, although this difference is modest.

The size of a parasitoid depends on the size of its host (Ris *et al.*, 2004), which also influences parasitoid fecundity. Therefore, we measured the sizes of *Drosophila* and of *Leptopilina*. For

Drosophila, PC1 accounted for 84.4% of the variance in wing size. *Drosophila* from Seattle had slightly bigger wings ($L1 = 2.103 \pm 0.0113$ mm) than did *Drosophila* from Igé (2.068 ± 0.0097 mm; $P = 0.025$). For size of *Leptopilina* (Fig. 1C), the best fitting model (Table 1) included fixed effects for source populations of both *Leptopilina* and *Drosophila*, but not their interaction ($P = 0.0991$). *Leptopilina* that emerged from Seattle *Drosophila* were larger than those that emerged from Igé *Drosophila* ($P \leq 0.001$). Inclusion of the *Leptopilina* source population slightly improved the model fit ($P = 0.040$): *Leptopilina* from Igé were slightly larger than those from Seattle. Overall, the main factor influencing the size of parasitoids was the source of host.

Leptopilina from Seattle had higher fecundity (Table 2) than did *Leptopilina* from Igé ($P \leq 0.001$) (Fig. 1B), independent of the source of the host *Drosophila* ($P = 0.37$). Fecundity was sensitive to the interaction between provenance of host and of parasitoid ($P = 0.0008$). Specifically, fecundity was relatively high when wasp and host came from the same locale, but relatively low when they came from different locales.

Table 1. Generalized linear mixed-effects model for variables associated with tibia length of *Leptopilina*

Model	<i>k</i>	log-likelihood	AIC	ΔAIC
<i>Drosophila</i> + <i>Leptopilina</i>	5	452.1	914.2	0* [#]
<i>Drosophila</i> * <i>Leptopilina</i>	6	450.7	913.4	-0.8
<i>Drosophila</i>	4	454.2	916.3	2.1*
<i>Leptopilina</i>	4	460.2	928.4	14.2 [#]
Null	3	461.9	929.8	15.6

Note: The model with the lowest AIC included an interaction for *Drosophila* and *Leptopilina* source populations, but did not significantly improve the fit over a model with *Drosophila* and *Leptopilina* but without an interaction ($P = 0.0991$). Thus we accept the simpler model. Its parameter values are intercept = 60.84, *Drosophila* = 1.8666, and *Leptopilina* = -0.9726.

* Likelihood ratio tests between these two models: $P = 0.0406$.

[#] Likelihood ratio tests between these two models: $P \leq 0.0001$.

Table 2. Generalized linear mixed-effects model for variables associated with fecundity of *Leptopilina*

Model	<i>k</i>	log-likelihood	AIC	ΔAIC
Tibia + <i>Drosophila</i> * <i>Leptopilina</i>	6	-208.3	428.5	0
<i>Drosophila</i> * <i>Leptopilina</i>	5	-222.5	455.1	26.6
<i>Drosophila</i> + <i>Leptopilina</i>	4	-228.2	464.3	35.8
<i>Leptopilina</i>	3	-229.9	465.8	37.3
Tibia	3	-245.4	496.7	68.2
Null	2	-259.9	521.9	92.4
<i>Drosophila</i>	3	-258.6	523.2	94.7

Note: The model with the lowest AIC included tibia length of *Leptopilina*, as well as source populations of *Drosophila* and *Leptopilina* and their interaction. This model was significantly better than all other models (all $P \leq 0.0001$). The parameter values are *Leptopilina* = 0.263, *Drosophila* = -0.0523, tibia = 0.0127, and interaction = 0.1550.

As noted above, the size of *Leptopilina* was influenced by the sources of *Drosophila* and of *Leptopilina*. Because fecundity increases with size (Eijs and Van Alphen, 1999), patterns of fecundity (Fig. 1B) might mainly be a function of differences in size of *Leptopilina* in the different treatments. In an exploratory analysis, we looked at fecundity versus size but without considering the effect of vial (Fig. 2A): no correlation was apparent ($P = 0.413$). However, when we used a mixed model to allow for the effect of vial (Fig. 2B), fecundity was strongly associated with tibia length ($P < 0.001$, mixed model, tibia vs. null model). The lack of correlation in Fig. 2A occurs because the among-vial variance is large and swamps the correlation. Clearly, including vial effects is important.

To determine whether size and source population influence parasitoid fecundity, we compared models for fecundity with tibia and source population in various combinations (Table 2). The best fitting model included tibia, *Drosophila*, *Leptopilina*, and the interaction between *Drosophila* and *Leptopilina*. Thus fecundity is influenced by source populations as well as by size.

DISCUSSION

The aim of the present study was to determine whether the success of *D. subobscura* in the Pacific Northwest (Beckenbach and Prevosti, 1986; Huey and Pascual, 2009) is related to escape from parasitoids, which cause major mortality in native Old World populations (Parsons, 1977; Janssen *et al.*, 1988; Driessen *et al.*, 1990; Boulétreau *et al.*, 1991; Fleury *et al.*, 2004, 2009). Before the present study, only one of two common European parasitoids (*Asobara tabida*) was known to occur in the Pacific Northwest, suggesting that *D. subobscura* there might enjoy partial escape (at least in terms of number of parasitoid species). However, we immediately discovered that a second European parasitoid (*Leptopilina heterotoma*) was common at our Seattle study site. Therefore, the success of *D. subobscura* in the Pacific Northwest is not due to a reduction in the number of species of parasitoids.

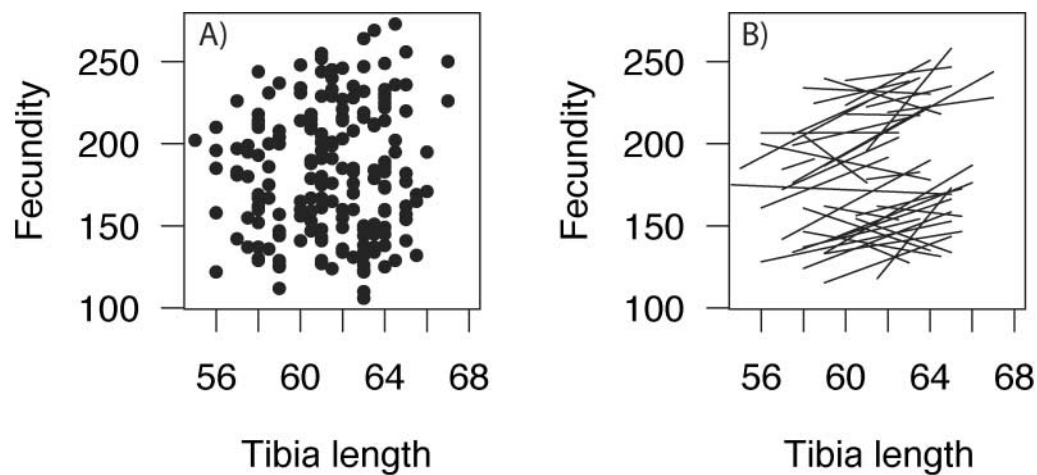


Fig. 2. (A) Fecundity of *Leptopilina* as a function of tibia length (mm*100) when the effect of vial is ignored. (B) Fecundity versus tibia length when the regression is plotted separately for each vial. The positive relation between fecundity and size is apparent only when vial is controlled for.

Partial escape from parasitism could still exist if American parasitoids are less effective at killing their hosts than are their French counterparts. This does not hold for *A. tabida* because these wasps kill more than 90% of all parasitized *D. subobscura*, whether in Europe or North America (Kraaijeveld and Van der Wel, 1994). However, *L. heterotoma* from North America might nonetheless be less successful than are those from France. To evaluate this possibility, we collected *D. subobscura* and *L. heterotoma* both in North America and in France and then measured parasitoid success in a factorial design (thus both allopatric and sympatric combinations). A similar protocol has been used previously [*L. boulardi*/*D. melanogaster* (Carton, 1984); *A. tabida*/*D. melanogaster* (Kraaijeveld and Godfray, 2001)].

We began by comparing parasitoid success rate, which is the probability that an infested host larva gives rise to an adult wasp (Boulétreau and Fouillet, 1982). However, success rate was not reduced for Seattle *L. heterotoma*; in fact, the success rate (SP) of *L. heterotoma* was high and remarkably similar (0.83–0.86) in all treatments. This may reflect the absence of an immune response in *D. subobscura* (Eslin and Doury, 2006; Havard *et al.*, 2009) (see ‘Concluding remarks’).

To compare the impact of parasitoids on flies, we computed the ‘degree of infestation’ (DI), which measures the proportional expected reduction in the number of flies emerging from a vial when a parasitoid was present (Boulétreau and Fouillet, 1982). Thus a high DI implies that parasitoids exerted heavy mortality, probably because both their attack and success rates were high. Degree of infestation was independent of the source population of host and parasitoid, but slightly sensitive to the interaction (Fig. 1A). Specifically, DI was relatively large if both host and parasitoid came from the same population. These results are consistent with local adaptation of parasitoid to host, but inconsistent with escape of *D. subobscura* from parasitoids.

Another way that North American *D. subobscura* could experience reduced parasitism would be if North American *L. heterotoma* had reduced fitness, which could occur if North American wasps were smaller and had lower fecundity than European wasps. In Europe, size and fecundity can vary in *L. heterotoma*, depending on the geographic origins of the parasitoid and of the host (Ris *et al.*, 2004).

We used tibial length to index parasitoid size. Female *L. heterotoma* were larger when reared on *Drosophila* from Seattle than on flies from Igé ($P \ll 0.001$; Fig. 1C). Females from Igé were slightly larger than those from Seattle ($P = 0.040$; Fig. 1C), but the interaction between host and parasitoid was not significant ($P = 0.099$). Overall, the main factor influencing parasitoid size was source of host. If ‘bigger is better’, then Seattle wasps have an advantage over Igé wasps, contrary to the escape hypothesis.

Fecundity of *L. heterotoma* females was strongly affected by the source of the parasitoids. Females from Seattle had much higher fecundity than did those from Igé ($P < 0.001$; Fig. 1B), was independent of host source ($P = 0.37$), but sensitive to an interaction between parasitoid and host source ($P < 0.001$; see below). The much greater fecundity of *L. heterotoma* from Seattle versus Igé (Fig. 1B) is surprising, even though fecundity of this species shows high variability between nearby populations in Europe (F. Fleury *et al.*, pers. comm.). In any case, the high reproductive (potential) output of Seattle parasitoids reared on Seattle hosts suggests that the success of *D. subobscura* in North America is unlikely to be a consequence of relatively low fitness of local *L. heterotoma*.

CONCLUDING REMARKS

A primary goal of our experiments was to evaluate the hypothesis that the success of invading *D. subobscura* reflects escape (or partial escape) from parasitoids. We found no support for that hypothesis. The number of parasitoid species of frugivorous *Drosophila* is the same as in France, parasitoid success rates and impacts are similar, and Seattle parasitoids are in fact more fecund. Of course, our experiments were conducted in the laboratory under artificial conditions. Potentially, field measures of parasitism rates at multiple sites and seasons might still show reduced effectiveness of parasitoids in the Pacific Northwest. Such field tests are feasible with these species (Janssen *et al.*, 1988; Allemand *et al.*, 1999; Fleury *et al.*, 2004).

It would be interesting to run parallel laboratory experiments on North American and European *D. melanogaster*, another important host for *L. heterotoma*. If *L. heterotoma* is a recent invader of North America, then local *D. melanogaster* (which presumably has been in North America for many generations) might still have low resistance. If so, the high success of *D. subobscura* could be the result of an indirect effect of the parasitoid on one of its competitors.

A second issue motivating our study was whether parasitoids show evidence of local adaptation to hosts. Surprisingly, local adaptation in host–parasitoid interactions has received little attention and has only been observed on *Drosophila* parasitoids in two other studies, *L. boucardi*/*D. melanogaster* (Carton, 1984) and *A. tabida*/*D. melanogaster* (Kraaijeveld and Godfray, 2001). In the present study, fecundity was relatively high when both wasp and host came from the same population (Fig. 1B), as evidenced by the significant interaction term. Thus *Leptopilina* appear locally adapted to their *D. subobscura* hosts – a pattern that has never been noted before.

The fact that parasitoid success rates and impacts were high and largely invariant among populations might be linked to the absence of resistance adaptations in *D. subobscura*. In many insects [including *melanogaster*-group *Drosophila* (Carton *et al.*, 1986)], the main internal defence is a cellular immune reaction in which host lamellocytes encapsulate the larval parasitoid, which dies by asphyxiation (see Nappi *et al.*, 2009). However, *obscura*-group flies either cannot encapsulate or only to a limited degree (Havard *et al.*, 2009); and *D. subobscura* in particular is unable to encapsulate either a parasitoid egg or even a foreign body (oil drop) (Eslin and Doury, 2006). Nevertheless, *D. subobscura* could potentially escape from parasitism by behavioural shifts that might reduce exposure to parasitoids, but such shifts remain to be studied.

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