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Comparative responses of two sympatric parasitoid cynipids to the genetic and epigenetic variations of the larvae of their host, *Drosophila melanogaster*

M. Boulétreau & E. Wajnberg
Laboratoire de Génétique des Populations (UA CNRS 243), Université Lyon I, 69622 Villeurbanne, France

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Abstract

Infestation of larvae of *Drosophila melanogaster* by both *Leptopilina boulardi* and *L. heterotoma* (Hymenoptera, Cynipidae: Eucoilidae) varies according to within-population genetic variations in the hosts. *L. heterotoma* larvae thrive better than *L. boulardi* and developmental success of both parasitoids varies according to the host's genotype. Crowding in hosts improves success rate of both species, that of *L. boulardi* then being equal to that of *L. heterotoma.*

Introduction

Host-parasitoid associations in insects involve a number of successive steps (Vinson, 1984). Host location and host selection (Vinson, 1976) occur prior to the actual parasitization and depend on the behavioural traits of both hosts and female parasitoids. The fulfilment of parasite larval requirements by the host are expressed in host suitability (Vinson & Iwantsch, 1980a) and host regulation (Vinson & Iwantsch, 1980b). The absence of immunological, biochemical and physiological barriers is an obvious condition for the full development of adult wasps.

The overall specificity of a parasite is determined by the flexibility of its response to different hosts and the success of a given parasite may vary within a host species. In the *Drosophila-Leptopilina* system, genetic variation exists between host populations (Walker, 1959; Carton, 1984, and pers. obs.). Within *Drosophila* populations, genetic heterogeneity has been demonstrated in the intensity of cellular defense reaction towards *Leptopilina boulardi* Barbotin *et al.* (Boulétreau & Fouillet, 1982; Carton & Boulétreau, 1985). Variations were also recorded in the rate of successful development of parasite larvae that have resisted to these immunological reactions (Boulétreau & Fouillet, 1982; Wajnberg *et al.*, 1985). Moreover, the nutritional condition of the host larvae greatly affects parasite development, and crowded hosts are more suited to *L. boulardi* larvae than are well-fed hosts (Prévost, 1985; Wajnberg *et al.*, 1985). Such differential sensitivity of hosts to their parasites has been credited with an important role in stabilizing host-parasite system (Hassell & Waage, 1984) and in regulating genetic and coevolutionary interactions (Clarke, 1976; Price, 1980; Barrett, 1984; Pimentel, 1984).

As populations of *Drosophila melanogaster* Meigen are infested by both *Leptopilina boulardi* and *L. heterotoma* Thomson in mediterranean regions (Rouault, 1979) and in the USA (Nordlander, 1980), we decided to extend results for *L. boulardi* to *L. heterotoma*, which is a more polyphagous species that thrives equally well in other Diptera (Jenni, 1951; Nostvik, 1954). Using the isofemale strains method (Parsons, 1980), we demonstrate that the success of these two related wasps, which exploit the same host population, depends strongly on the individual host's genotype and nutritional condition. Both species show the same type of response, but with different intensities, to variations in their hosts.

Material and methods

Our strains of *D. melanogaster, L. boulardi* and *L. heterotoma* originated from Tunisia. Both parasite species infest their hosts in similar ways: the females lay eggs inside the 2nd instar host larvae, which continue to develop and pupate. At 25 °C, adult wasps emerge from the host's puparium 18 to 20 days after parasitization for *L. boulardi,* 19 to 21 days for *L. heterotoma.* Only one parasite develops inside each host. In these Tunisian strains, *Drosophila* larvae do not exhibit cellular defense reaction against their parasites.

Fifteen pairs of adult flies, taken from a laboratory mass rearing, were used to establish fifteen isofemale strains of *D. melanogaster.* At the next generation, 14 batches of 100 eggs were collected from each strain. After hatching and first moulting, six of these batches were each exposed to one *L. boulardi* female and six other batches to one *L. heterotoma* female over a 24-h period. All parasite females were taken from a standardized laboratory rearing and were 24-h old at the time of infestation. Two control batches were kept free of parasites.

Out of the six batches infested by each parasite species for each *Drosophila* strain, three were allowed to develop in vials containing 20 g of rich medium (David & Clavel, 1965) (uncrowded series), the three others in dishes containing only 1.5 g of the same medium diluted by half (crowded series). Thus, three tests were run simultaneously under both developmental conditions and for both parasite species in each host strain. Unparasitized batches were treated in the same way to measure the total viability of uninfested hosts in crowded and uncrowded cultures. The whole experimental procedure is summarized in Fig. 1.

After proper development (25 °C, L12:D12 h), the numbers of adult flies and parasites emerging from each vial were recorded and used to calculate two quantitative parameters:

Degree of infestation (D.I.). This parameter measures the percentage of infested larvae in each experimental batch. In the absence of efficient defense reaction against parasites, no host larva survives being parasitized. The number of infested hosts may thus be estimated from the difference between the numbers of flies emerging from infested batches and from the uninfested control batches:

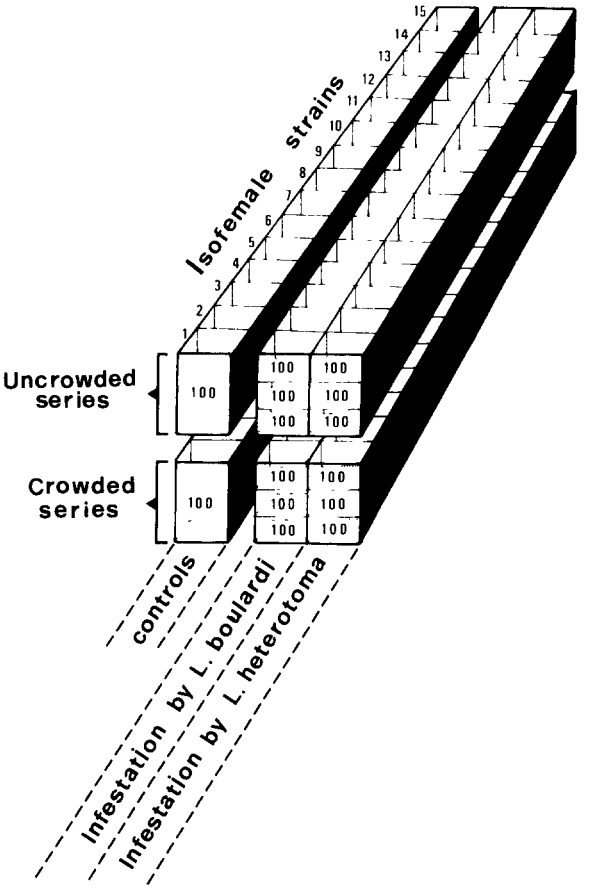

Fig. 1. Diagrammatic representation of the experiments. In each isofemale host strain, batches of 100 individuals are either kept free of parasites (controls) or infested by *L. boulardi* or *L. heterotoma.* Hosts are developed either uncrowded, or crowded.

D.I. (%) = 100. (flies in control batches − flies in infested batches)/(flies in control batches).

Rate of success of parasite development (R.S.P.D.). This parameter is measured by the proportion of infested hosts that give rise to an adult wasp. It is expressed by the ratio of the number of emerged wasps to the number of infested hosts estimated as above: RSPD (%) = 100. emerged wasps/infested hosts. This parameter is taken as a measure of overall host suitability.

More detailed parameters can be used in quantitative studies on parasitism (Carton & Kitano, 1981; Carton, 1984). However, we prefer the two mentioned above for two reasons. First, their estimation needs no handling or larval dissection and

allows the manipulation of large numbers (here: 21000 *Drosophila* larvae). Secondly, their biological meaning is quite clear; the D.I. expresses the probability of a given host of being parasitized, and the R.S.P.D. expresses the probability of a parasitized host giving rise to a wasp.

Results

Measurements done on control host batches play an important part in the parameters used to estimate the outcome of parasitism. Their reliability is discussed below.

Crowding did not affect the egg-to-adult viability of uninfested hosts ($85.9 \pm 1.8\%$ in controls, $81.5 \pm 2.2\%$ in crowded series, $F = 2.5$, N.S.). However the size of emerging flies was significantly reduced in crowded series (thorax length of males: 92.2 ± 0.3 1/100 mm in controls, 81.2 ± 0.6 in crowded series, $P < 0.01$).

There were two controls for each strain, one exposed to crowding, and the other not. This allows the statistical analysis of the observed variations. Variance analysis shows that the between-strains variations are far higher than the within-strains variations, which however include the non-significant effect of crowding ($F = 7.5$, $P < 0.01$). The stability of viability within each host strain is further attested by the correlation ($r = 0.78$, $P < 0.01$) and regression ($b = 1.01$) coefficients between values measured in the crowded and uncrowded batches.

The numbers of flies emerging from the control batches are used in the calculation of both D.I. and R.S.P.D., and variability of the former could introduce a bias in the latter. However no correlation exists between viability in controls and either the D.I. ($rs = -0.03$, N.S.) or the R.S.P.D. ($rs = -0.16$, N.S.). Thus variations in these parameters actually measure variability in the outcome of parasitism.

Tables 1 and 2 show that in standardized tests, *L.*

Table 1. Degree of infestation (D.I.) and rate of success of parasite development (R.S.P.D.) by *L. boulardi* and *L. heterotoma* in uncrowded and in crowded hosts. Each replicate involves 100 host larvae.

		L. boulardi		*L. heterotoma*	
		D.I. (%)	R.S.P.D. (%)	D.I. (%)	R.S.P.D. (%)
Uncrowded series	$\bar{x}$	74.93	40.21	67.74	78.05
	s.e.	3.51	2.43	3.77	2.30
	n	45	42	45	42
Crowded series	$\bar{x}$	73.16	89.35	59.23	88.10
	s.e.	2.03	1.44	3.55	1.87
	n	45	45	45	41

Table 2. Analysis of variance of Degree of Infestation (D.I.) and of Rate of Success of Parasite Development (R.S.P.D.). Variances are calculated after arc sin $\sqrt{p}$ transformation. (*): $P < 0.05$; (**): $P < 0.01$).

Source of variation	D.I.			R.S.P.D.		
	d.f.	Variances	F	d.f.	Variances	F
Wasp species (1)	1	2559.24	10.57 (**)	1	6973.23	64.38 (**)
Devt conditions (2)	1	538.77	2.22 (NS)	1	21155.75	195.32 (**)
Host strains (3)	14	503.29	2.07 (*)	14	228.30	2.11 (*)
Interaction (1)-(2)	1	294.74	1.21 (NS)	1	6692.37	61.79 (**)
Interaction (1)-(3)	14	470.87	1.94 (NS)	14	103.93	<1
Interaction (2)-(3)	14	259.55	1.07 (NS)	14	239.87	2.21 (**)
Interaction (1)-(2)-(3)	14	173.57	<1	14	161.95	1.49 (NS)
Error	120	242.09		110	108.31	
Total	179	291.32		169	337.35	

boulardi females infested hosts significantly more than *L. heterotoma;* on average, 74.0% of larvae were infested by *L. boulardi,* and only 63.5% by *L. heterotoma.* Moreover, levels of parasitism by either parasite varied significantly between host strains.

The success of parasite development (RSPD) depends on wasp species, host genotype and developmental conditions;

Wasp species. In normally-fed host larvae (uncrowded series), larvae of *L. heterotoma* thrive two times better than those of *L. boulardi* (78% v. 40%, Tables 1 and 2).

Host genotype. The success of parasite development varies significantly between host strains (Tables 1 and 2). In Fig. 2, lines are ordered according to decreasing values of RSPD to show for each condition and parasite species the range of variation, for *L. boulardi:* 25–63%, for *L. heterotoma:* 62–92%. Responses of both species are correlated as shown in Fig. 3, thus demonstrating that parasite success depends on intrinsic features of each host strain.

Developmental conditions. The crowding of hosts strongly enhances the development success of both parasites (Table 2 and Fig. 2). The success of *L.*

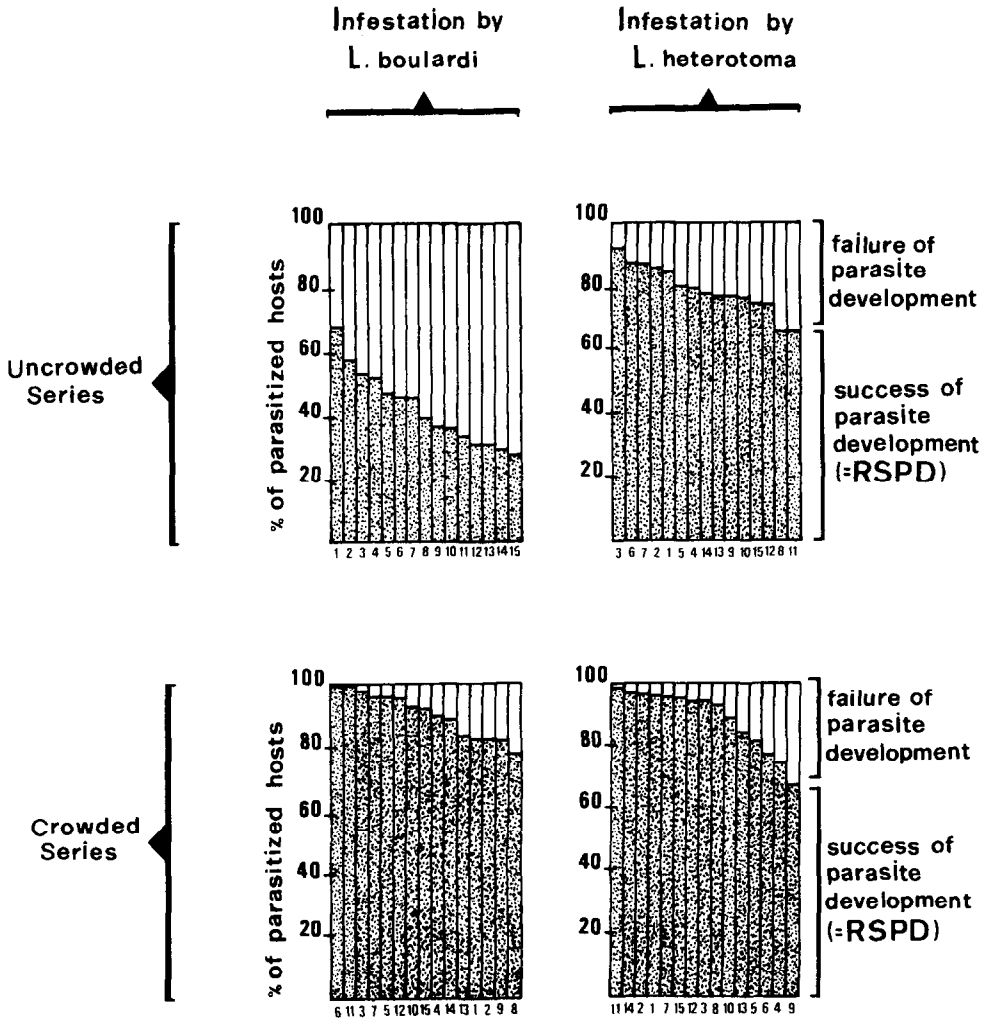

Fig. 2. Rate of success of development of *L. boulardi* and *L. heterotoma* in uncrowded and in crowded hosts. R.S.P.D.: % of parasitized hosts. Column: the average of 3 replicates (3×100 hosts) in a given host strain. Strains ordered according to decreasing values of RSPD.

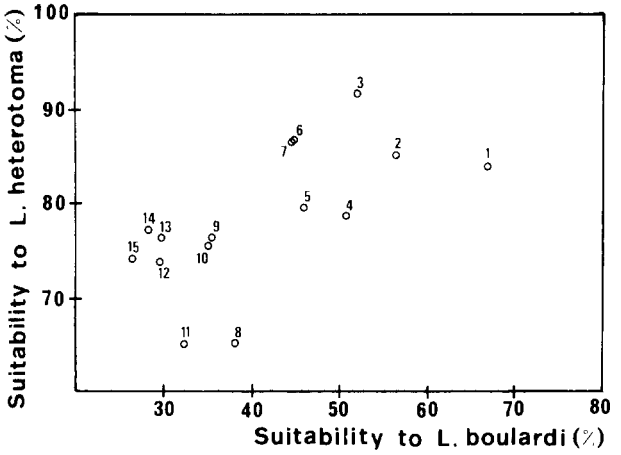

Fig. 3. Correlation between suitability of *Drosophila* larvae for *L. boulardi* and for *L. heterotoma* in uncrowded series. Points: *Drosophila* isofemale strains. Lines numbered as in Fig. 2. Spearman correlation coefficient: $r_s = 0.675$, $p < 0.05$).

boulardi larvae then reaches that of *L. heterotoma* larvae (88 v. 89%).

Discussion

Our results demonstrate that variations in the hosts modify their responses to parasitism by *L. boulardi* and *L. heterotoma.* Two important steps are affected: host infestation and parasite development.

The mean rates of infestation are different with both wasp species. In the experimental conditions here adopted, *L. boulardi* is twice as efficient as *L. heterotoma* at infesting hosts, but of course the greatest care must be taken in extending this conclusion to field situations.

More interesting are the slight but significant between-strains variations in the degree of infestation that were not detected in previous experiments involving only *L. boulardi* and lower numbers of replicates (Boulétreau & Fouillet, 1982; Wajnberg *et al.,* 1985). Host selection by insect parasitoids is a complex process involving a number of steps (see Vinson, 1984 for a review). Variations in the degree of infestation may result from fluctuations in nature or the intensity of stimuli emanating from the hosts. For instance, the probability for *Drosophila* larvae of being parasitized by a Braconid wasp, *Asobara tabida,* depends on frequency of larval movements (Van Alphen & Drijver, 1982).

Another hypothesis, not exclusive of the former, considers variations of resource utilization by host larvae. The larval foraging behaviour of *Drosophila* larvae, especially their digging behaviour, is genetically determined (Godoy-Herrera, 1977; Sokolowski, 1982). Behavioural differences between laboratory strains are correlated to differences in the level of infestation by *L. boulardi* (Carton & David, 1985); deeper burrowing larvae could get some protection against attack from female parasites. Variations in the foraging behaviour of *Drosophila* larvae (Bauer & Sokolowski, 1984) could account for differences in rates of infestation here observed.

The absence of significant interaction between wasp species and host strains (see Table 2) shows that both parasites exhibit similar responses to variations in their hosts, despite small differences in their host-searching behaviours (Vet, 1984).

The success rate of parasite development exhibits striking variations with regards to wasp species, host's genotype and the crowding of host larvae. The failure of parasite development is accompanied by death of the host. This phenomenon is quite different from the elimination of *L. heterotoma* eggs by *Drosophila* species of the *melanica* group (Nappi, 1970; Nappi & Streams, 1970); in these species, parasite eggs or larvae are eliminated without visible reaction of the hosts, which actually recover from parasitism. The failure observed, corresponding to death of the whole parasite-host system, illustrates the excessive pathogenic effects of the parasite on its host. These effects can be explained by two hypotheses.

First, death of the parasitized larvae could be due to poisoning by venom injected by female wasps at the time of oviposition (Gerling & Rotary, 1973). Different toxicities of venom of both species, and variations in sensitivity of hosts to these venoms, could easily account for differences in mortality among uncrowded parasitized larvae. However, it can hardly be accepted that post-parasitism crowding should reduce the larval's sensitivity to poisoning. Samson-Boshuizen *et al.* (1974) have reported the death of *Drosophila* larvae after being parasitized by *L. heterotoma.* However, the phenomenon is restricted to very early oviposition attempts by newly-emerged females, and the killed

host larvae generally do not contain parasite eggs. In our experiments, most killed larvae did contain a parasite, as demonstrated by high numbers of wasps emerging from crowded series. Thus, if poisoning by female venom cannot be totally excluded, its role is probably limited and it cannot be responsible for the high mortalities among larvae parasitized by *L. boulardi* and for their variations.

A second hypothesis considers the nutritional suitability of host, and the regulation of hosts by their parasites (Vinson & Iwantsch, 1980a, 1980b). Improper fulfilment of parasite requirements by the host, are improper synchronism between the physiological evolution of growing hosts and parasite larvae, could provoke the death of one of the partners, which in turn could be responsible for death of the other. Higher mortalities among *Drosophila* larvae parasitized by *L. boulardi,* and higher between-strains variations could simply express greater requirements of *L. boulardi.* This hypothesis is consistent with the broader host range of *L. heterotoma* (Jenni, 1951; Nostvik, 1954).

The physiology and growth of *Drosophila* larvae are greatly affected by crowding and underfeeding (Bakker, 1961; David *et al.,* 1971). It is possible that crowded hosts are more easily regulated by growing parasites, or that their contents and their physiology better suit to parasite's requirements, thus enhancing the success of parasite development.

The probability of parasitism and the suitability for development of the parasites are not evenly distributed within host population. Thus, the host population is not homogeneous with regard to the susceptibility to parasitism by both wasp species. It is generally admitted that differential sensitivity to parasitism plays a major role in the dynamics of host-parasite systems and conditions the occurence of genetic and coevolutionary interactions (Clarke, 1976; Barrett, 1984; Hassell & Waage, 1984). The *Drosophila – Leptopilina* system is a good material for experimental studies in this field, which has been poorly documented in insects (Boulétreau & Fouillet, 1982; Carton & Boulétreau, 1985; Wajnberg *et al.,* 1985).

The observed variation range within host population is far wider than between different populations (Carton, 1984 and pers. obs.). Thus, in the species studied here, host suitability as a component of host specificity is to be considered at the genetic level rather than at the population or the species level. Moreover, host suitability is strongly influenced by nutritional factors, and comparison between parasite species leads to contrary conclusions depending on whether well-fed or crowded hosts are considered.

Despite the lack of reliable field data, we attempt to discuss the significance of our results to field situations. The parasite species studied here are sympatric in their natural breeding site (Tunisia), where they seem to exploit mainly larvae of *D. melanogaster* and *Drosophila simulans* sturtevant (pers. obs.). Our results suggest that if they compete for host exploitation, the outcome could be affected by crowding of hosts. Abundant resources could favour establishment of *L. heterotoma,* which develops in well-fed hosts better than *L. boulardi.* The scarcity of resources, leading to underfeeding of host larvae, allows *L. boulardi* to develop as well as *L. heterotoma.* Then a greater efficiency in host searching could favour *L. boulardi.*

Therefore, seasonal variations of resource abundance for hosts could partly account for variations in the relative abundance of both parasite species, a phenomenon that seems to actually occur in the field (Carton, in litt.). Temporal fluctuations in the organization of this host-parasite community could thus be partly explained by seasonal variations of food abundance for the host.

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Résumé

Réponses comparées de deux Cynipides parasitoides sympatriques aux variations génétiques et épigénétiques de leur hôte, Drosophila melanogaster

Les résultats de l'infestation des larves de *D. melanogaster* par les Cynipides *Leptopilina boulardi* et *L. heterotoma* varient selon le génotype

des hôtes et leur état nutritionnel. L'analyse génétique de la population hôte par la méthode des lignées isofemelles montre que le degré d'infestation (pourcentage de larves effectivement parasitées dans des tests standidardisés) varie significativement entre lignées. Le taux de succès du développement parasitaire (pourcentage d'hôtes parasités fournissant un parasite adulte) est plus élevé chez *L. heterotoma* que chez *L. boulardi* et varie fortement entre lignées d'hôtes. Les variations chez les deux parasites sont corrélées.

La sous-alimentation des larves parasitées augmente le succès du développement des deux parasites et celui de *L. boulardi* devient alors égal à celui de *L. heterotoma.*

La réponse à l'infestation par les deux Cynipides n'est pas uniforme au sein de la population hôte et varie en fonction de l'abondance des ressources nutritionnelles de ce dernier.

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