

## GENETIC AND EPIGENETIC VARIATION IN *DROSOPHILA* LARVAE SUITABILITY TO A HYMENOPTEROUS ENDOPARASITOID

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Suitability of *Drosophila melanogaster* larvae to their endoparasite *Leptopilina bou-  
lardi* (Nordlander, 1980) shows wide genetic and epigenetic variation. Experiments  
were done on *Drosophila* isofemale lines. When reared in optimal laboratory condi-  
tions only 50 % of parasitized *Drosophila* larvae gave rise to an adult wasp, and  
significant variation was observed between lines. In crowded conditions, this ave-  
rage value increased up to 90 % and no more significant variability could be detec-  
ted between lines. Genetic and demographic consequences of these results are dis-  
cussed.

KEY-WORDS : *Drosophila* parasites - Host suitability - Genetic variability - Nutri-  
tional influences.

An obvious condition for parasitic association in insects is host suitability (Vinson, 1976 ;  
Vinson & Iwantsch, 1980a, 1980b), which expresses fulfilment by hosts of the requirements  
of parasitic larvae. Accuracy of this fulfilment shows variations in any given host-parasite  
system. Epigenetic influences, such as nutritional conditions, may modify host suitability  
(Vinson & Iwantsch, 1980a). Genetic variation also occurs between (Chabora, 1970a,  
1970b ; Carton & Kitano, 1981 ; Carton, 1984) and within populations (Boulétreau &  
Fouillet, 1982). We decided to measure how underfeeding and larval competition interact  
with genetic determinism in fixing the level of suitability of *Drosophila melanogaster* larvae  
to their endoparasitoid *Leptopilina boulardi* (Nordlander, 1980).

### MATERIAL AND METHODS

Female parasites lay their eggs inside 2nd instar *Drosophila* larvae which continue to  
develop and pupate. At 25°C adult wasps emerge from host's puparia on days 18-20 after  
parasitization. Only 1 parasite develops inside each host. Both *Drosophila melanogaster* and  
*Leptopilina boulardi* strains originated from Tunisia. In these strains, *Drosophila* larvae do  
not exhibit cellular defense reaction against their parasites.

Ten lines of *D. melanogaster* were established, each from a pair of adult flies taken from  
the laboratory mass-rearing. At the next generation, 6 batches of 100 eggs were collected  
from each line. When 24-48 h old, larvae hatched from these eggs were exposed to parasiti-  
zation for 24 h (1 *L. boulardi* female/batch).

Of the 6 batches infested simultaneously in each *Drosophila* line, 3 were allowed to develop at 25°C in vials containing 20 g of rich medium (David & Clavel, 1965) (uncrowded series), the 3 others in dishes containing 1.5 g of the same medium diluted by half (crowded series). Controls (1 for each line and for each developmental condition) kept free of parasites allowed the measure of overall survival in crowded and uncrowded uninfested cultures.

The outcome of each test depends upon 2 distinct features of host-parasite relationships.

Firstly, the proportion of host larvae actually parasitized by the wasp is a consequence of behavioural interactions between the female parasite and their hosts. Since only unparasitized *Drosophila* larvae give rise to flies, the degree of infestation of the larval host population (DI) was calculated from the difference between numbers of flies emerging from uninfested and infested cultures :

$DI = 100 \times (\text{flies from uninfested batch} - \text{flies from infested batch}) / (\text{flies from uninfested batch})$ .

Secondly, the number of emerging wasps depends on the proportion of parasite larvae which fully developed in their hosts. It is a consequence of physiological interactions between host larvae and their endoparasites. Failure of development of the latter leads to the death of both host and parasite. The probability of parasitized host giving rise to an adult parasite was measured by the rate of success of parasite development (RSPD) :

$RSPD = 100 \times \text{emerged wasps} / \text{infested hosts}$ .

This parameter was considered as a measure of host suitability.

In each line and under both developmental conditions, 3 tests were run simultaneously. Variation within and between lines was thus measured for each parameter under both developmental conditions.

TABLE 1

*Egg to adult survival and size of emerging males in crowded and uncrowded controls kept free of parasites*

	Uncrowded series ( $\bar{x} \pm \text{s.e.}$ )	Crowded series ( $\bar{x} \pm \text{s.e.}$ )	F
Survival (%)	85.85 $\pm$ 2.16 (10 replicates)	84.45 $\pm$ 2.14 (10 replicates)	< 1
Wing length (1/100 mm)	219.13 $\pm$ 1.47 (30 flies)	201.47 $\pm$ 1.31 (30 flies)	151.02 (a)
Thorax length (1/100 mm)	92.23 $\pm$ 0.32 (30 flies)	81.20 $\pm$ 0.62 (30 flies)	249.92 (a)

Estimation of survival rate is based on 10 replicates involving each 100 individuals, and variances for this trait are calculated after arc sin  $\sqrt{p}$  transformation on percentages.

(a)  $p < .01$ .

## RESULTS

Table 1 shows that crowding did not affect overall survival in uninfested controls. However size reduction in adult males demonstrates that crowding and/or underfeeding did occur.

Table 2 shows that degrees of infestation were the same in crowded and uncrowded series, and did not exhibit significant variations between lines. They can thus be considered as homogeneous over the whole experiment.

TABLE 2

*Variability of degree of infestation (DI) and of rate of success of parasite development (RSPD) in uncrowded and crowded series*

Uncrowded series					Crowded series				
	Mean	Variance			F	Mean	Variance		
		total (df)	within (df)	between (df)			total (df)	within (df)	between (df)
DI	83.25 %	121.21 (26)	123.48 (17)	116.69 (9)	< 1	78.46 %	159.93 (24)	130.28 (16)	219.22 (8)
RSPD	51.50 %	42.58 (26)	26.72 (17)	72.55 (9)	2.715 (a)	89.64 %	220.89 (24)	241.64 (16)	179.40 (8)

Variances are calculated after arc sin  $\sqrt{p}$  transformation on percentages.

(a)  $p < .05$

Table 2 and fig. 1 show that rate of success of parasite development is strongly increased by crowding ( $p < .001$ ). The overall variation in this trait increased much more within lines than between lines. As a result, no significant variation was detected between lines in crowded series. On contrast, the suitability of *Drosophila* larvae to the parasite varied significantly between lines in uncrowded series. No correlation existed between values obtained for the crowded and the uncrowded series (Spearman correlation coefficient  $r_s = .2$ , N.S.).

## DISCUSSION

Host suitability is important at a theoretical level, as well as at an applied one, because it plays a major role in the regulation of host and parasite populations (Pimentel & Stone, 1968; Price, 1975; Carton, 1984).

The present results indicate that host suitability is determined by both genetic and epigenetic factors.

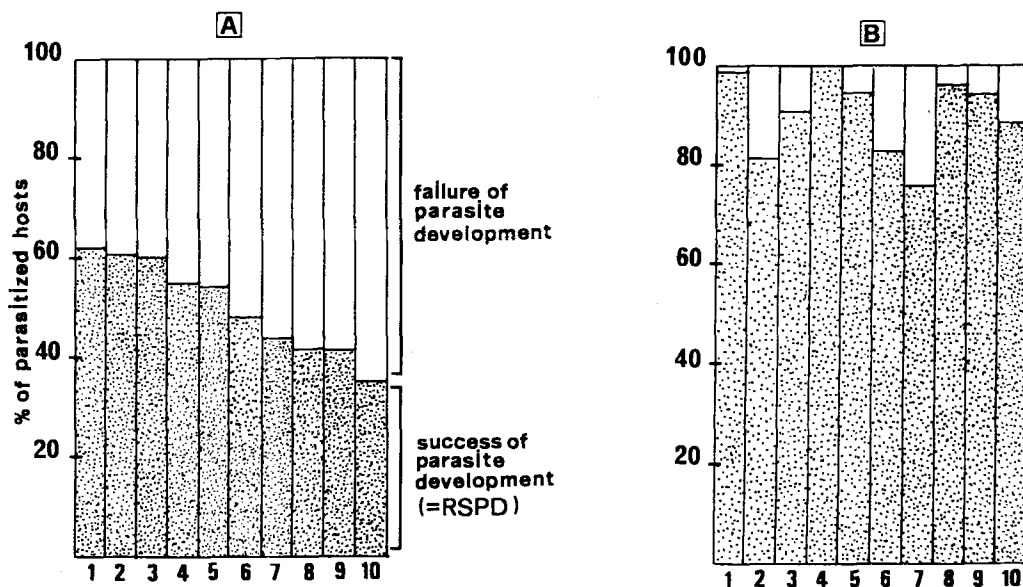


Fig. 1. Rate of success of parasite development (RSPD) in 10 *Drosophila* lines. A. uncrowded series ; B. crowded series. In both graphs, lines are arranged in decreasing values of RSPD as measured in uncrowded series (A).

Within-population genetic variation of host suitability, already demonstrated in other *Drosophila* populations (Boulétreau & Fouillet, 1982), seems to be a regular phenomenon in the *D. melanogaster*-*L. bouleaudi* association. The range of variation here recorded between lines from the same population was wider than the range of variation between mean values of different host populations (Carton, 1984, and pers. observ.). Existence of such a variation in long coevolved populations suggests that it is maintained, directly or indirectly, by active genetic mechanisms, and its role in coevolutionary processes must be taken into consideration.

Increase of host suitability in crowded cultures is a surprising result, which is due to physiological changes in starving and/or crowding hosts and which has not yet been explained satisfactorily. This epigenetic factor could also play an important role in demographic interactions between hosts and parasites, since for a given initial level of infestation, larval populations of *Drosophila* give rise to many more adult wasps when underfed.

These 2 causes of variation make it difficult to attribute a distinct value of suitability to a particular host-parasite system.

In natural populations, suitability of *Drosophila* larvae to *L. bouleaudi* depends on availability of nutritional resources and hence, could change in time. For a given population, suitability in the field may be quite different from suitability as measured in standardized laboratory conditions, and comparison of populations based on laboratory tests must be prudent.

Moreover, low suitability of a number of *Drosophila* lines within the population is likely to exert a strong selective pressure on parasites, which are selected for increasing their ability to succeed their infestation. Since all *Drosophila* larvae became suitable hosts when underfed, it may be concluded that strength of genetic interactions between host and parasite is not constant but depends on availability of nutritional resources.

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## RÉSUMÉ

Variations génétiques et épigénétiques de l'adéquation  
de la *Drosophila* à un endoparasitoïde hyménoptère

L'adéquation des larves de *Drosophila melanogaster* à leur parasite *Leptopilina boulardi* (Nordlander, 1980) montre d'importantes variations génétiques et épigénétiques. Les expériences ont été réalisées sur des lignées isofemelles de drosophiles. Dans les conditions optimales de développement en laboratoire, en moyenne 50 % des larves de drosophiles parasitées conduisent à l'émergence d'un parasite adulte, et une variation significative est observée entre les lignées. En condition de surpeuplement, cette valeur moyenne atteint 90 %, et aucune variabilité significative n'est observée entre les lignées. Les conséquences génétiques et démographiques de ces résultats sont discutées.

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