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Journal

Genetica, 70(1)

ISSN

0016-6707

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Publication Date

1986-08-01

DOI

10.1007/BF00123215

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Intra- and intergenotypic competition in *Drosophila melanogaster*: effects of density on larval survival and rate of development

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Abstract

We have examined the effects of density and frequency in the larval competition of *Drosophila melanogaster* by measuring three fitness components: viability (V), mean development time (MDT) and a combination of these two (E). We have detected (contrary to most published results) non-linear effects of density in single-genotype cultures; in addition, different functions are required to describe the density effects below and above the optimal density. Frequency has also non-linear effects in the two-genotype cultures. Only one polymorphic equilibrium frequency, which is stable, occurs with respect to V; but two polymorphic equilibria, one stable and one unstable, exist with respect to E. The responses in single-genotype cultures do not allow one to predict the outcome of the competition in two-genotype cultures.

Introduction

The 'optimal density' (D) of a growing population with limited resources may be defined as that initial number of individuals that yields the maximum number of survivors (Wilson, 1980; Wallace, 1981). In the case of larval competition studies, optimal density may be redefined taking into account viability (V) and mean developmental time (MDT), two fitness components showing density dependence (Barker & Podger, 1970; Caligari, 1980; Mather & Caligari, 1981).

The competitive fitness of different genotypes has been shown to depend on the density and the frequency of the competing genotypes (De Wit, 1960; Ayala, 1972; DeBenedictis, 1977; Harper, 1977; Mather & Caligari, 1981; Wallace, 1981; Tosić & Ayala, 1981). The experiments of Bakker (1961, 1969) with *Drosophila melanogaster* indicate that the response of two genotypes competing in a single culture ('bicultures') can be predicted from their performance in separate cultures ('monocultures'). The experiments herein reported are designed to test this relationship with respect to op-

timal density, D, and to ascertain whether the density response is or not linear (Clarke & O'Donald, 1964; De Jong, 1976; Snyder & Ayala, 1979; Nunney, 1983).

Material and methods

Two strains of *Drosophila melanogaster* are used: Oregon-R (Or) and an eye-colour mutant (herein called *m*), captured in a wine cellar near Requena (Valencia, Spain). The two strains are kept in 250 ml bottles with 50 ml of food medium, at 25 °C and 60% relative humidity.

The procedure to obtain large numbers of same-age larvae is as follows. Adults are placed in a culture bottle for 24 h, and then transferred to a bottle without medium where they are exposed to egg-collection 'layers' for 12 h. The layers are watch glasses with a medium made of agar, water, acetic acid and ethanol, to which a few grains of yeast are added. The layers are cut in pieces with 150 to 200 eggs, which are placed in 250 ml bottles with 50 ml of food. When the adults emerged are 5-days

old, they are transferred again to fresh culture bottles for 48 h, after which they are exposed to layers for 4 h. These layers are kept in Petri dishes for 18 h, when the larvae are collected and transferred to competition vials. These larvae are of similar age (a range of 4 h) and are progenies of parents of similar age (a range of 12 h).

The biculture competition vials are 40×8 mm with 0.5 ml of food, seeded with 70 larvae. Competition is intense under these conditions but mortality due to food desiccation is not excessive. The initial densities in the monocultures are:

m: 4 10 20 35 60 66 70

Or: 70 66 60 50 35 10 4

The genotypic combinations in the bicultures are:

m/Or: 4/66 10/60 20/50 35/35 60/10 66/4

All density combinations for mono- and bicultures are done simultaneously, and are replicated 20 times.

V and MDT are measured by counting the number of adults emerging for the vials every second day from the 11th until the 25th day after the larvae are seeded.

Models

Optimal density for viability

Optimal density (*D*) is defined as the input number of larvae that yields a maximum number of survivors. This number divides the input density range into two: (1) below the optimal density the resources are not fully used; (2) above that density, the resources are not sufficient for the development of all the larvae. In terms of Wallace's (1982) concept of 'biological space unit', *D* corresponds to the complete, non-competitive utilization of these units; densities below *D* leave unused units, those above *D* require that some units be occupied by more than one individual.

In order to estimate *D* we use a polynomial fit:

$$V = a \pm b_1 N \pm b_2 N^2 \pm \dots, \quad (1)$$

where $V = n/N$, *N* is the input number of larvae, and *n* is the output number of adults emerged. After the fit is accomplished, we obtain numerically the maximum of the following function:

$$n = N (a \pm b_1 N \pm b_2 N^2 \pm \dots). \quad (2)$$

If Wallace's (1981) notion of biological space units is correct, *V* should be constant below *D*, but vary above *D*. We have two models, of which the first one, but not the second, assumes that *V* is constant below *D*:

Model I: for $N \leq D$, $V = \text{constant}$; for $N > D$, $V = f(N)$

Model II: for $N \leq D$, $V = g(N)$; for $N > D$, $V = h(N)$.

The polynomial fit of either one of the models may require a polynomial function with a degree higher than one.

Optimal density for viability and development time

The optimal density models just proposed do not take into account the rate of emergence of the adult flies, which is nevertheless an important contributor to fitness. We adopt the following optimality principle: 'the largest number of adults emerged in the shortest possible time gives the best fitness'. We introduce a fitness parameter, *E*, with a maximum that maximizes simultaneously viability, *V*, and the reciprocal of the mean development time, MDT, as follows:

$$E_{\max} = \max \left(V \cdot \frac{1}{\text{MDT}} \right). \quad (3)$$

The function adopted for *E* is:

$$E = \sum_{i=0}^k V_i \cdot \frac{1}{T_i}, \quad (4a)$$

where *i* indexes the number of days since the larvae are seeded in the vial, and $T_i = t_i/t_{\text{optimal}}$, where *t_i* is the number of days from larva to adult, and $t_{\text{optimal}} = 10$ because that is the minimum number of days from larva to adult in our cultures. Hence,

$$E = \sum_{i=0}^k V_i \cdot \frac{10}{t_i}. \quad (4b)$$

Let *s_i* be the number of adults emerged in the *i*-th day, so that $V_i = s_i/N$. Then, for computational purposes we can use

$$E = \frac{10}{N} \sum_{i=0}^k \frac{s_i}{t_i}. \quad (4c)$$

The density giving the optimal fitness is, therefore, the input number that gives a maximum N.E.

Statistical methods

We have analyzed our results by analyses of variance supplemented with polynomial regression, using the method of Bancroft (1964; see Draper & Smith, 1981) to decide the significance of the regression parameters. The larva-to-adult viability is transformed as follows:

$$V' = \arcsin \sqrt{(n+3/8)/(N+3/4)}. \quad (5)$$

The added values of 3/8 and 3/4 are convenient given that in some cases $N < 10$ (Ashcombe, 1948). For numerical computation, we use:

$$n = (N+3/4) \sin^2(a \pm b_1 N \pm b_2 N^2 \pm \dots) - 3/8. \quad (6)$$

The value of N which yields the first maximum n is taken as the optimal density, D .

When the variances are heterogeneous, the data are reanalysed following the method of Sokal & Rohlf (1969, p. 372–73; see Snedecor & Cochran, 1967).

Results

Monocultures

Table 1 gives the transformed viability (V'), the mean development time (MDT, in days) and the fitness (E) for the two strains, m and Or, in single-strain cultures. The results of the analyses of variance are shown in Table 2. Density has a significant effect for all three parameters in both strains. The values of the parameters of the most significant re-

Table 1. Mean and standard error for transformed viability (V'), development time (MDT, in days) and fitness (E) in monocultures of two strains, m and Or, of *Drosophila melanogaster*.

Initial density	m			Or		
	V'	MDT	E	V'	MDT	E
4	60.6 ± 2.6	14.13 ± 0.15	0.5602 ± 0.0333	63.9 ± 3.3	15.10 ± 0.41	0.5720 ± 0.0462
10	62.0 ± 2.6	14.64 ± 0.15	0.5340 ± 0.0257	61.1 ± 2.3	15.58 ± 0.35	0.5006 ± 0.0293
20	58.1 ± 1.1	15.04 ± 0.13	0.4854 ± 0.0125	–	–	–
35	55.6 ± 1.5	15.26 ± 0.09	0.4489 ± 0.0149	52.9 ± 2.9	16.33 ± 0.19	0.3934 ± 0.0331
50	–	–	–	44.9 ± 2.2	16.87 ± 0.16	0.3035 ± 0.0242
60	43.4 ± 1.5	16.27 ± 0.13	0.2929 ± 0.0156	37.2 ± 1.6	17.39 ± 0.17	0.2130 ± 0.0164
66	40.6 ± 0.8	16.13 ± 0.11	0.2660 ± 0.0091	34.2 ± 1.6	17.46 ± 0.15	0.1864 ± 0.0152
70	36.9 ± 1.1	16.52 ± 0.14	0.2209 ± 0.0113	30.5 ± 1.6	17.63 ± 0.29	0.1549 ± 0.0152

Table 2. Analysis of variance for transformed viability (V'), development time (MDT) and fitness (E) for each two strains, m and Or, of *Drosophila melanogaster* in monocultures. The analysis assumes that the variances are heterogeneous, as shown by a Bartlett's test.

Fitness component	Source of variation	m				Or			
		SS	df	MS	F	SS	df	MS	F
V'	Density	348.2	6	58.04	54.88***	211.2	6	35.21	33.50***
	Error	61.2	58	1.06		62.0	59	1.05	
	Total	409.4	64			273.2	65		
MDT	Density	96.0	6	16.00	47.48***	69.9	6	11.65	11.01***
	Error	44.5	132	0.30		61.3	58	1.06	
	Total	140.5	138			131.2	64		
E	Density	475.6	6	79.27	74.96***	209.2	6	34.86	32.98***
	Error	61.3	58	1.06		61.7	58	1.06	
	Total	536.9	64			270.9	64		

*** $P < 0.001$.

Table 3. Parameter values for the polynomial regression and optimal density (D) for each of three fitness components in two strains of *Drosophila melanogaster*. R^2 measures the proportion of the experimental variance explained by the regression.

Fitness component	<i>m</i>			Or		
	Parameter values	R^2	D	Parameter values	R^2	D
V'	$a = 61.2245$ $b_1 = -0.0018$ $b_2 = -0.0024$	0.994	55	$a = 64.0869$ $b_1 = -0.1218$ $b_2 = -0.0021$	0.997	49
MDT	$a = 14.2095$ $b = 0.0225$	0.968	-	$a = 14.8521$ $b_1 = 0.0554$ $b_2 = -0.0003$	0.992	-
E	$a = 0.5896$ $b = -0.0035$	0.985	59	$a = 0.5894$ $b = -0.0043$	0.991	48

gression are given in Table 3, together with the optimal densities calculated from them, both for viability alone and for viability plus development rate (=fitness).

Figure 1 shows the functions derived multiplying by N either the viability per individual (V) or the fitness (E). The optimal density derived from E should be smaller than the one derived from V ,

Fig. 1. Output viability (V') and fitness (E) as a function of the input densities for the monocultures of two strains (*m* and Or) of *Drosophila melanogaster*. The predicted function as well as the experimental points are shown. The vertical dash lines indicate the optimal input density (D).

Table 4. Analysis of variance for the polynomial regression functions in two density ranges ($N < D$ and $N \geq D$) for two fitness components (V' and E) in two strains of *Drosophila melanogaster*.

Fitness component	Range	Source of variation	<i>m</i>				Or			
			SS	df	MS	F	SS	df	MS	F
V'	$N < D$	Density	477.18	3	159.06	1.89	1306.27	2	654.13	3.92*
		Error	6386.59	76	84.03		9503.09	57	166.72	
		Total	6863.77	79			10809.36	59		
	$N \geq D$	Density	413.35	2	206.67	7.47**	2258.27	3	752.76	12.39***
		Error	1549.12	56	27.66		4617.63	76	60.75	
		Total	1962.47	58			6875.90	79		
E	$N < D$	Density	0.14	3	0.05	4.41**	0.33	2	0.16	5.99**
		Error	0.79	76	0.01		1.55	57	0.03	
		Total	0.93	79			1.88	59		
	$N \geq D$	Density	0.05	2	0.026	7.81***	0.25	3	0.08	12.41***
		Error	0.18	56	0.003		0.50	76	0.01	
		Total	0.23	58			0.75	79		

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

given that E is the product of the viability times the developmental function and both are smaller than one. In the case of the m strain, however, that is not the case due to the fact that the two polynomial regressions are of different degrees (only the first-order regression parameter is significant for developmental time).

Table 4 gives the analyses of variance separately for the ranges $N < D$ and $N \geq D$. In the case of the m strain, the effects of density for the viability function are not significant, which means that Model I is appropriate in this case (i.e., V may be assumed to be constant for $N < D$). Model II, however, is required for the fitness function of the m strain as well as for both the viability and the fitness function of the Or strain.

Bicultures

The transformed viabilities, mean development time, and fitness values for the two strains competing together are given in Table 5. The ANOVA results are given in Table 6. Comparison of Tables 1 and 5 shows that, generally, there is competition between the strains at all densities. The exceptions are densities 60 and 66 at which the Or strain has better viability and development rate when competing with m than in monoculture.

Frequency-dependence is explored following the approach of Sokal & Karten (1964) and Snyder & Ayala (1979). The values of the significant parameters are given in Table 7. Mean development time is constant for both strains and so is fitness for m .

Table 5. Mean and standard error of three fitness components (V' , MDT, and E) in bicultures of two strains, m and Or, of *Drosophila melanogaster*.

Initial densities		V'		MDT		E	
<i>m</i>	Or	<i>m</i>	Or	<i>m</i>	Or	<i>m</i>	Or
4	66	59.79 $\pm$ 3.29	41.49 $\pm$ 1.39	15.67 $\pm$ 0.36	16.01 $\pm$ 0.16	0.2479 $\pm$ 0.0339	0.1675 $\pm$ 0.0114
10	60	47.21 $\pm$ 2.12	44.53 $\pm$ 0.76	15.80 $\pm$ 0.24	16.03 $\pm$ 0.12	0.2105 $\pm$ 0.0310	0.1691 $\pm$ 0.0124
20	50	42.84 $\pm$ 1.94	46.52 $\pm$ 1.01	15.77 $\pm$ 0.19	16.57 $\pm$ 0.11	0.1698 $\pm$ 0.0333	0.1837 $\pm$ 0.0179
35	35	37.55 $\pm$ 1.61	45.92 $\pm$ 1.33	15.60 $\pm$ 0.18	17.01 $\pm$ 0.12	0.1528 $\pm$ 0.0211	0.2441 $\pm$ 0.0255
60	10	40.42 $\pm$ 0.75	48.99 $\pm$ 3.41	16.47 $\pm$ 0.13	16.69 $\pm$ 0.29	0.2238 $\pm$ 0.0116	0.2249 $\pm$ 0.0266
66	4	38.54 $\pm$ 0.84	60.59 $\pm$ 3.36	16.59 $\pm$ 0.13	16.40 $\pm$ 0.37	0.2121 $\pm$ 0.0095	0.4251 $\pm$ 0.0356

Table 6. Analysis of variance for three components in bicultures of *Drosophila melanogaster*. The analysis assumes that the variances are heterogeneous, as shown by a Bartlett's test.

Fitness component	Source of variation	<i>m</i>				Or			
		SS	df	MS	F	SS	df	MS	F
V'	Density	14.61	5	2.92	2.77*	57.58	5	11.52	10.95*
	Error	53.81	51	1.06		54.78	52	1.05	
	Total	68.42	56			112.36	57		
MDT	Density	6.75	5	1.35	1.28	7.43	5	1.48	1.42
	Error	48.69	46	1.06		55.17	53	1.04	
	Total	55.43	51			62.60	58		
E	Density	11.53	5	2.30	2.19	56.58	5	11.32	10.76*
	Error	53.78	51	1.05		54.67	52	1.05	
	Total	65.31	56			111.25	57		

* $P < 0.05$.

Table 7. Parameter values of the polynomial regression for frequency dependence in bicultures of *Drosophila melanogaster*. R^2 gives the fraction of the experimental variance explained by the regression.

Fitness component	<i>m</i>		Or	
	Parameter values	R^2	Parameter values	R^2
V'	a = 41.3807 b ₁ = -0.4865 b ₂ = 0.0048	0.856	a = 50.8217 b = -0.2081	0.673
MDT	c [†] = 15.98	-	c [†] = 16.45	-
E	a = 0.2654 b ₁ = -0.0043 b ₂ = 4.1×10^{-5}	0.863	c [†] = 0.2357	-

† MDT has a constant value for both strains, E is constant only for Or.

The viability of Or is linearly frequency-dependent, whereas the frequency dependence is quadratic for both the viability and the fitness of the *m* strain. In all cases, the performances of the two strains are separately analyzed (Wright, 1969; Nei, 1971; Cockerham *et al.*, 1972).

In order to determine possible equilibrium points and their stability, we have estimated relative fitness functions (Lewontin, 1958) assuming that the only components contributing to fitness are the parameters herein measured. The results are shown in Table 8 and Figure 2.

The viability function gives one polymorphic equilibrium point (with the *m* frequency at $p=0.188$), which is stable. The fitness (E) function

yields two polymorphic equilibria, one stable ($p=0.074$) and the other unstable ($p=0.962$). The rate of development is not significantly frequency dependent: the Or strain is superior to the *m* strain at all frequencies.

Table 8. Equilibrium frequencies of *m* predicted by the functions and their stability characteristics.

Fitness component	Equilibrium frequencies	Stability
V'	0.1883	stable
MDT	0	neutral
E	0.0744	stable
	0.9615	unstable

Discussion

Wallace's (1981) 'unit biological space' and Maynard Smith's (1974) territory are concepts that imply the existence of an optimal density for a group of organisms with a defined set of resources. The optimum occurs when all limiting resources are used but there is no shortage of them. When the organisms share the same genotype, the optimum represents the density below which the viability is constant; when the density is greater than the optimum, the viability decreases. If the concept of optimal density just given is correct, then Model I should also be correct: viability starts to change only when the available resources are not sufficient for all the individuals present ($N > D$). On the contrary, if competition already exists below the optimal density ($N < D$), then Model II would be appropriate (the presence of two different functions of N , delimited by $N = D$, may be justified if the intensity of the competition is qualitatively different below and above that density). Whether or not Model I is sufficient may depend on the particular system considered. In any case Model I as well as Model II assume that viability is not density-dependent linear, and therefore that the output function is not a symmetric parabola, contrary to what is assumed by some models of populations growth, including the logistic function (e.g., Mather & Caligari, 1981; Wallace, 1981). It may be that a linear density response appears to be the case in some studies, because the number of densities explored is not sufficiently large.

The parameter E that we have proposed is a measure of the rate at which adults emerge, obtained by combining viability and rate of development. Although these two fitness components are related ($MDT = (1/V) (\sum_{i=0}^k s_i t_i / N)$), the responses obtained will be different when the process is only density-dependent (in which case their correlation will be higher) and when it is also frequency-dependent. The interaction between these two

Fig. 2. Population dynamics predicted by the frequency-dependent relative fitnesses of two competing strains, $\underline{m}$ and $\underline{O}$, of *Drosophila melanogaster*. The arrows indicate the polymorphic equilibrium points, which may be stable (S) or unstable (U).

parameters could be, of course, explored with relationships other than the multiplicative one assumed in the definition of E , given that one parameter might be considered more important than the other in particular circumstances.

Can one predict the competition between two strains from the separate study of the strains? Not so in our case. At densities of a given strain above 35 the m strain has better viability than the Or strain in the monocultures, but not in the bicultures. Moreover, such prediction is not possible when interstrain competition is frequency dependent, as it is for viability as well as for fitness in our experiments. Frequency-dependence with respect to larval viability has been repeatedly detected (Sokal & Hubert, 1963; Sokal & Karten, 1964; DeBenedictis, 1978; Snyder & Ayala, 1979; Anxolabéhère, 1980; Mather & Caligari, 1981; Tosic & Ayala, 1981). But there have been few attempts to detect frequency dependence with respect to rate of development (Barker & Podger, 1970). Yamazaki (1971) did not detect it for the *est-5* locus in *Drosophila pseudoobscura*. Snyder & Ayala (1979) had some indication of it, but the frequency-dependence was not statistically significant. We also have failed to detect frequency dependence with respect to mean development time. Although V and MDT are related, which is reflected in the fact that the monoculture responses are similar for both (see Table 3), their response in the bicultures is quite different: MDT is constant whereas viability is not and has first degree (Or) and even second degree (m) significant parameters (see Table 7). This discrepancy may, of course, be due in part to the relatively large variance of MDT ; with additional frequency combinations, a non-constant response might be detected for MDT in the bicultures.

Linear as well as non-linear frequency dependence have been the subject of extensive theoretical investigation (Haldane & Jayakar, 1963; Clarke & O'Donald, 1964; Wright, 1969; Cockerham *et al.*, 1972; Asmussen, 1983). But there have been few demonstrations of non-linear frequency dependence in the past (DeBenedictis, 1977; Anxolabéhère & Périquet, 1981). This may have been due in part to the methods used — such as ratio diagrams and linear regression, which are not geared to detect non-linear responses even if they exist (DeBenedictis, 1977; Inouye & Schaffer, 1981).

An important implication of non-linear frequen-

cy dependence is that it can generate more than one polymorphic equilibrium. In our case, there is one (stable) polymorphic equilibrium for viability, but two (one stable and one unstable) for the fitness function that integrates viability and development time.

The polynomial functions used in our models make it possible to detect non-linear responses, as indeed we have uncovered. The conclusions often reached that linear responses are sufficient to account for the competition process may be dependent on the fact that alternative, non-linear models have not been explored. We believe that lack of non-linear response should not be generally assumed unless nonlinearity can be excluded by appropriate statistical tests.

Acknowledgement

This work has been partly supported by a grant of the 'Comité Conjunto Hispano-Norteamericano para la Cooperación Cultural y Educativa'.

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Received 17.7.1985 Accepted 4.12.1985.