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Overcompensation as a mechanism for maintaining polymorphism: egg-to-adult viability in *Drosophila*

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Abstract

Frequency-dependent selection may be accounted for, in ecological terms, by the differential effectiveness of alternative genotypes in exploiting limiting environmental resources. Differentiation in resource exploitation among genotypes implies in turn that a mix of genotypes may exploit more fully the resources than a genetically uniform population, a phenomenon called 'overcompensation'. Experiments designed to test for overcompensation show that highly polymorphic populations can support larger numbers of individuals per food unit than less polymorphic populations. This difference cannot be attributed to the level of individual heterozygosity, which is the same in both types of populations.

Introduction

Frequency-dependent selection is often invoked as a process maintaining genetic polymorphism. Frequency-dependence may arise as a consequence of predator selection, as pointed out by Fisher (1930) for Batesian mimicry; by mate choice, as in the case of rare-mate advantage discovered by Petit (1951); through competition for resources (Ayala, 1968, 1971); and in other ways (Ayala & Campbell, 1974). In particular, whenever there is competition for limiting resources, a negative correlation between the frequency of genotypes and their fitness may be accounted for if alternative genotypes exploit different resources, or exploit them differentially. If such is the case, as one genotype becomes more common the environmental resources that it exploits exclusively or best become more saturated, so that the genotype increasingly competes for resources that are best exploited by the alternative genotypes. It follows that the relative fitness of the genotype that is becoming increasingly common gradually decreases. If this explanation is correct, it follows that the limiting resources will be

better exploited by a mix of several genotypes than by only one genotype (Levins, 1965; Ayala, 1972). This phenomenon has been called 'overcompensation' (see Tošić & Ayala, 1980 and references therein).

The present experiments were designed to test the phenomenon of overcompensation in *Drosophila melanogaster* by measuring the rate of egg-to-adult survival. Populations that are highly polymorphic are compared with populations that are more nearly monomorphic, but so that the individuals are equally heterozygous in both types of populations. The tests are done at two densities, one at which there should be none or very little competition for food ('scant' cultures) and another at which competition exists ('crowded' cultures). The *Sod* locus (which codes for copper-zinc superoxide dismutase) is used as a genetic marker.

Material and methods

Several hundred *Drosophila melanogaster* females collected in El Rio Vineyard (San Joaquin County,

California) were placed in individual vials. Sib-pair matings were made in separate vials with their progenies. After oviposition, the mating pairs were assayed by gel electrophoresis; the progenies of those pairs with desired *Sod* genotypes were again used to prepare sib-pair matings. The process was repeated for four generations so as to obtain 10 stock strains homozygous for the *F* allele and 10 homozygous for the *S* allele, each of which was descended from a different wild female. These stock strains were represented as 1F, 2F, ... 10F; 1S, 2S, ... 10S. The experiments were started about 1-2 months after the stock strains were prepared.

Crosses were made among the strains according to the following pattern in order to produce zygotes that would not be inbred, but rather carry two genomes derived from two different wild-collected flies and, hence, would be similar in this sense to zygotes in nature. With respect to the *Sod* locus the zygotes were of three kinds: homozygotes *F/F*, which were progenies of the crosses 1F♀ × 2F♂, 2F♀ × 3F♂, ... 10F♀ × 1F♂; homozygotes *S/S*, from the crosses 1S♀ × 2S♂, 2S♀ × 3S♂, ... 10S♀ × 1S♂; and heterozygotes, from the crosses 1F♀ × 6S♂, 2F♀ × 7S♂, ... 5F♀ × 10S♂; or 6S♀ × 1F♂, 7S♀ × 2F♂, etc.

Two levels of polymorphism were created in the experiments: 'low' and 'high'. In the low-polymorphism populations, all eggs in a vial came from parental females from a single strain crossed to males from a different strain. All 10 stock strains of a given *Sod* genotype were, however, equally represented in each experimental block.

In the high-polymorphism populations, 10 different stock strains were represented in each vial. Thus, in a set homozygous for the *S* allele, the eggs in a given vial came from 10 different crosses between the 10 *S* strains, each strain represented by an equal number of eggs. Similarly, in a set homozygous for the *F* allele, the eggs in a given vial came from all 10 different *F* strains. In each *F/S* vial, the eggs were progenies of females from five *S* or five *F* strains (e.g., 1S, 2S, ... 5S) each crossed to males from one of five strains with different *Sod* genotype (e.g., 6F, 7F, ... 10F).

Notice that the average individual heterozygosity was the same in the low- and in the high-polymorphism cultures. The developing flies had in all cases the mother coming from one stock strain and the

father from a different stock strain (and thus they had a degree of heterozygosity comparable to wild-collected flies, since they carried two genomes independently sampled from a natural population). What was different, was the level of population polymorphism, since the genomes of only two stock strains were represented in each low-polymorphism vial, whereas the genomes of 10 different stock strains were represented in each high-polymorphism vial.

The low-density conditions ('scant' cultures) were created by placing 30 eggs in a large vial (2.5 × 10 cm) with 15 ml of medium. In the high density conditions ('crowded' cultures), 150 eggs were placed in a small vial (2 × 8 cm) with 10 ml of medium. 20 replicate vials were prepared at the low density for each *Sod* genotype and level of polymorphism; 10 replicate vials at the high density for each *Sod* genotype and level of polymorphism.

The culture medium in the experimental vials was a standard cornmeal-and-molasses *Drosophila* medium, the same used for the crosses and to maintain the stocks. All cultures were kept in an incubator at 25 ± 0.5°C, ca. 70% relative humidity, and a 12 h. light/darkness cycle.

Results

The experimental results are summarized in Table 1. The analyses of variance of the arc sine-transformed data are given in Table 2.

Table 1. Egg-to-adult viability (percent with standard errors) in cultures with either high or low background polymorphism at two densities. The number of replicates is N = 20 for low-polymorphism experiments and N = 10 for high-polymorphism experiments.

Polymorphism	Genotype	Density	
		Scant	Crowded
Low	<i>F/F</i>	83.0 ± 1.7	66.3 ± 1.4
	<i>F/S</i>	84.0 ± 2.5	73.3 ± 1.8
	<i>S/S</i>	82.8 ± 2.3	59.8 ± 2.1
	Average	83.2 ± 0.3	66.5 ± 3.9
High	<i>F/F</i>	83.0 ± 2.8	79.9 ± 2.5
	<i>F/S</i>	84.3 ± 3.8	75.5 ± 2.5
	<i>S/S</i>	85.7 ± 2.8	70.7 ± 2.4
	Average	84.3 ± 0.8	75.4 ± 2.7

Table 2. Two-way analyses of variance within each level of polymorphism. The data are arc sine-transformed.

Polymorphism	Source of variation	SS	df	MS	F
Low	Density (D)	1.2674	1	1.2674	90.52***
	Genotype (G)	0.1837	2	0.0918	6.56**
	D × G	0.0942	2	0.0471	3.36*
	Error	1.5962	114	0.0140	
High	Density (D)	0.3436	1	0.3436	20.67***
	Genotype (G)	0.0047	2	0.0024	0.14
	D × G	0.0272	2	0.0136	0.82
	Error	0.8977	54	0.0166	

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

Density has a statistically significant effect at both levels of polymorphism. The rate of egg-to-adult survival is 83 to 86% at low density, but considerably lower, 60 to 80%, at the higher density. The *Sod* genotype has a significant effect in the low-polymorphism cultures, but not in the high-polymorphism cultures. The analysis of variance shows that there is a significant interaction between genotype and density in the low-polymorphism cultures. This interaction is apparent in Table 1: the viability of all three *Sod* genotypes is very similar in the uncrowded cultures, whereas there is overdominance in crowded conditions. Table 3 gives the results of *t*-tests for pairwise comparisons between different *Sod* genotypes. Under crowded conditions, the heterozygotes have significantly greater viability than either one of the two kinds of homozygotes in low-polymorphism cultures; moreover, the homozygotes for the more common allele in nature (*F/F*) are superior to the homozygotes for the allele that is rarer in natural populations (*S/S*).

Table 1 shows that when competition is minimized or absent (scant cultures), there is no difference in rate of survival between the low- and the high-polymorphism cultures. However, under the competitive conditions of the crowded cultures, the rate of survival is higher in the highly polymorphic cultures. Table 3 shows that this difference is statistically significant for two of the three *Sod* genotypes, as well as for the overall average.

Table 3. *t*-tests for the difference in egg-to-adult viability between *Sod* genotypes.

Polymorphism	Genotypes compared	df	Density	
			Scant	Crowded
Low	<i>F/S-F/F</i>	38	0.58	3.82***
	<i>F/S-S/S</i>	38	0.57	5.58***
	<i>F/F-S/S</i>	38	0.04	2.63*
High	<i>F/S-F/F</i>	18	0.46	0.22
	<i>F/S-S/S</i>	18	0.28	1.37
	<i>F/F-S/S</i>	18	0.80	1.11

* $P < 0.05$; *** $P < 0.001$

Table 4. *t*-tests for the difference in egg-to-adult viability between high-polymorphism and low-polymorphism cultures.

Genotype	df	Density	
		Scant	Crowded
<i>F/F</i>	28	0.00	5.29***
<i>F/S</i>	28	0.07	0.70
<i>S/S</i>	28	0.70	3.22**
Average	88	1.50	2.68**

** $P < 0.01$; *** $P < 0.001$

Discussion

Fisher (1930) may have been the first to show explicitly that a genetic polymorphism may occur as a consequence of frequency-dependent selection. In a dimorphic Batesian mimic, he argued, there will be an inverse relationship between the selective advantage of each form and its frequency. The analysis of the selective process in experimental *Drosophila* populations moved Levene *et al.* (1954) to suggest that the selective value of a genotype might generally be dependent upon its frequency. This was emphatically asserted by Kojima (1971) in a paper entitled 'Is there a constant fitness value for a genotype? No!' Frequency-dependent selection may occur with respect to one or more fitness components and as a consequence of interactions with the physical environment or with other organisms of the same or different sex and of the same or different species (reviews in Ayala & Campbell, 1974; Clarke & Partridge, 1988).

The statement that the selective value of a particular genotype is frequency dependent implies a mathematical relationship between the frequency of that genotype and its fitness, but it says by itself nothing about the underlying causation. Tošić and Ayala (1980, p. 64) have argued that 'with respect to viability, [a] negative correlation between the frequency of genotypes and their fitness can be accounted for, in ecological terms, if alternative genotypes exploit different environmental resources, or exploit them differentially'. Whenever resources are limiting, as the frequency of a type increases the resources it exploits better become depleted and, hence, it has to compete for resources that are better exploited by its competitors. The fitness of the type under consideration will consequently decrease as it becomes more common. An interesting implication of this process is that, other things being equal, a polymorphic population will exploit limiting resources better than a monomorphic one, because at the polymorphic equilibrium the heterogeneous resources are each exploited by the type best able to use it. This is the phenomenon of overcompensation. It is this logical implication of frequency-dependent fitness that our experiments were set to test. Frequency-dependent fitnesses have been numerous demonstrated in cases of competition for resources, but few instances exist where the underlying processes have been elucidated or where overcompensation has been shown to occur in animals (see, however, Tošić & Ayala, 1980; Peng *et al.*, submitted).

The results herein reported show that, when there is competition for limiting resources, the proportion (and number) of first-instar larvae able to develop into adults is greater when the level of polymorphism is higher. On the average, the proportion of survivors is 75.4% in the high-polymorphism cultures, but 66.5% in the low-polymorphism cultures (Table 1, last column) and the difference is statistically significant (Table 4, last column). The difference in viability is also statistically significant for the homozygotes *S/S* and *F/F* considered separately, although not for the heterozygotes. No effect attributable to different levels of polymorphism exists, however, in the 'scant' cultures, where there is no competition for resources and 83-85% of all first-instar larvae develop into adult flies.

As pointed out earlier, the level of individual heterozygosity is the same in the low as in the high-polymorphism cultures: the developing flies in the former are full siblings of those in the latter. What is different is the level of population polymorphism: progenies of several mated pairs are present in each of the high-polymorphism cultures, but only the progeny of one mated pair in each low-polymorphism culture. Thus, the increased productivity of the high-polymorphism cultures under competitive conditions is clearly due to overcompensation; i.e., it must be attributed to the increased genetic diversity of the population per se, not to the heterozygosity of individuals. Nor should the productivity differences be attributed to different arrays of genotypes being present in the high- and low-polymorphism cultures, since collectively the two sets include the same genotypic arrays: the high-polymorphism include in each culture genotypic arrays that are distributed among several cultures in the low-polymorphism set.

Tošić and Ayala (1980) and Peng *et al.* (submitted) have carried out experiments specifically designed to test for overcompensation in *D. pseudoobscura* and *D. melanogaster*, respectively. Overcompensation was demonstrated in both cases. In the experimental design used in those two studies, viability and fertility effects could not be disentangled from one another. In the present experiments, however, the overcompensation effects are exclusively due to larval competition for resources. Moreover, we created two densities, a lower one at which competition would not occur (or be extremely low). As expected, overcompensation does not occur when competition for resources is absent. Notice that the 'low' density in the *D. melanogaster* experiments of Peng *et al.* (and also in the *D. pseudoobscura* experiments of Tošić & Ayala, 1980) is much higher – and involves larval competition for food – than in the present experiments. Thus at the low density of Peng *et al.*, the number of adult flies emerging per vial ranges from 61 to 88 individuals, whereas in the experiments herein reported the initial scant density is 30 larvae per vial.

The significance of overcompensation as a process maintaining genetic polymorphisms in natural populations remains to be determined. That overcompensation can so readily be demonstrated in the laboratory suggests that it may be a common phe-

nomenon in nature. Overcompensation brings also new light to the calculations of 'genetic load' sometimes used as an argument against the selective maintenance of multiple genetic polymorphisms. When alternative genotypes differ in selective value, a polymorphic population will necessarily have lower average fitness than the fitness of the most fit genotype. This reduction in fitness creates a genetic 'load' that becomes increasingly greater as the number of loci maintained by selection increases. Overcompensation makes the genetic load argument paradoxical. A polymorphic population carries a genetic load but may exploit better the environment, and be able to maintain a larger population, than a monomorphic population. Better exploitation of the environment may occur not only on the average, but also with respect to the fittest genotype. Peng *et al.* (submitted; see their Tables 1 and 8) have shown in *D. melanogaster* that mixed populations with three *Sod* genotypes exhibit overcompensation with respect to each one of the three genotypes separately considered.

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