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Fertility and viability at the *Sod* locus in *Drosophila melanogaster*: non-additive and asymmetric selection

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Summary

Experiments were designed to test in *Drosophila melanogaster* the effect of mating type at the *Sod* locus on fertility and viability. The experiments show that fertility is neither additive (or multiplicative) nor symmetric, i.e. that the fertility of a mating type cannot be predicted from the average fertility of the two genotypes involved in the mating. There is no significant male × female interaction with respect or progeny viability; but the interaction is significant for productivity, i.e. when fertility and viability are jointly taken into account. There is overdominance with respect to female fertility, but not with respect to male fertility or to viability. There also is alloprocoptic selection with respect to fertility and with respect to productivity, i.e. matings between like homozygotes are less fertile and productive than matings between dissimilar homozygotes. Selection at the *Sod* locus yields stable polymorphic equilibria, with the frequency of the *F* allele predicted at $P = 0{\cdot}641$ or $0{\cdot}695$, respectively for low and high larval density.

1. Introduction

Fertility is one of the most important fitness components, as has become apparent particularly over the last two decades (Moya, Latorre, & Ayala, 1989, and references therein). Fertility models, however, generally assume (1) additivity (or multiplicativity), i.e. that the fertility of a mating-pair type can be predicted from the separate fertilities of the two mating genotypes (e.g. Bodmer, 1965) and (2) symmetry between matings with respect to sex, so that the fertilities of ♀A × ♂B and ♀B × ♂A are the same (e.g. Hadeler & Liberman, 1975; Clark & Feldman, 1986). These assumptions are made, of course, for the sake of simplicity and, in the case of mathematical models, so as to reduce the number of parameters. There is, however, substantial experimental evidence that neither of the two assumptions obtains, but rather that fertility may be a property of the mating type – i.e. determined by specific interactions between the two mating genotypes, not predictable from the average fertility of the two genotypes involved (Moya & Ayala, 1989; Moya, Latorre & Ayala, 1989). This situation is of considerable import for the maintenance of genetic polymorphism, because when such interactions between mating genotypes occur, more than one stable polymorphic equilibrium is possible (Hadeler & Liberman, 1975; Moya, Latorre & Ayala, 1989).

Serradilla & Ayala (1983*a*, *b*) designed experiments specifically to test the assumptions mentioned above of additivity and symmetry, and found them both wanting with respect to each of several loci coding for enymes in *Drosophila melanogaster*. Moreover, they discovered the phenomenon of alloprocoptic selection, namely that the fertility of a mating type is greater than expected when the two mating individuals are homozygous for different alleles but smaller when both mates are homozygous for the same allele. Alloprocoptic selection is a form of balancing selection, because it tends to favor the persistence of genetic polymorphism.

In the present paper we report an experiment designed to test in the *Sod* locus of *D. melanogaster* whether fertility is (1) determined by mating type and (2) alloprocoptic. We carry forward the balancing-selection consequences of these hypotheses by measuring (3) the viability of the zygotes produced by each mating type. The experiments are also designed to test (4) whether overdominance exists with respect to fertility and viability. The *Sod* gene, which codes

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for copper-zinc superoxide dismutase, is used as the target locus because these experiments are intended as part of an extensive program addressed to investigate the molecular, population-genetic, and evolutionary characteristics of the *Sod* locus.

2. Materials and methods

(i) *Strains*

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 strains homozygous for the *S* allele, each of which was descended from a different wild female. These stock strains are represented as 1F, 2F,... 10F; 1S, 2S,... 10S. The experiments were started about 1–2 months after the stock strains were prepared. The frequencies of the *F* and *S* alleles in the natural population sample were 0·873 and 0·127, respectively.

(ii) *Culture conditions*

Stock strains and experimental cultures were all kept at 25 ± 0·5 °C and *ca.* 70% relative humidity in vials with a standard cornmeal-and-molasses *Drosophila* medium. Vials were either 'small' (2 × 8 cm, with 10 ml of culture medium) or large (2·5 × 10, with 15 ml of medium).

(iii) *Fertility*

Crosses were made among the strains according to the following pattern in order to obtain adult flies that would not be inbred, but rather carry two genomes derived from two different wild-collected flies and, hence, be similar in this respect to flies in nature. Homozygotes *F/F*: 1F♀ × 2F♂, 2F♀ × 3F♂,..., 10F♀ × 1F♂. Homozygotes *S/S*: 1S♀ × 2S♂, 2S♀ × 3S♂,..., 10S♀ × 1S♂. Heterozygotes: 1F♀ × 2S♂, 2F♀ × 3S♂,..., 10F♀ × 1S♂.

Three virgin females were collected from a given cross and placed with three virgin males collected from a different cross. After 6 days, the six flies were transferred to a cylindric plexiglas tube that had a small Petri dish with charcoal-coloured medium attached at one end and a cotton plug at the other end. This was done at 07.00 h on day 6, and again on day 7, after eclosion; at 14.00 h the Petri dish was removed and the eggs counted.

Fertility was measured as the number of eggs laid by three females in two consecutive days (6th and 7th post-eclosion) between 07.00 and 14.00 h. If any of the three females or three males died before 14.00 h on day 7, the vial was replaced.

There are nine possible mating-type combinations among the three genotypes. Each combination was replicated 20 times by using five specific strain combinations for each mating type at a given time and repeating the experiment at four different calendar times. The strain combinations used are as follows (representing by 1F. 2F the progenies of 1F♀ × 2F♂, and similarly for other interstrain crosses). *F/F*♀ × *F/F*♂: 1F.2F♀ × 6F.7F♂, 3F.4F♀ × 8F.9F♂, 5F.6F♀ × 10F.1F♂, 7F.8F♀ × 2F.3F♂, 9F.10F♀ × 4F.5F♂. The *S/S*♀ × *S/S*♂ and the *F/S*♀ × *F/S*♂ were combined according to the same pattern. In the other six mating types the females and males were also derived from the same particular interstrain combinations. The purpose of this design was to insure that there would not be inbreeding effects that might yield spurious genotypic differences. Indeed, the males as well as the females the fertility of which is measured carry each two genomes derived from two different wild flies and, hence, are genetically comparable to flies directly sampled from a natural population.

(iv) *Egg-to-adult viability*

Eggs collected from a given mating type were placed in groups of 30 per large vial (low density experiments) or in groups of 150 per small vial (high density experiments). Each combination was replicated 45 times, so that the experiment consisted of 9 mating types × 2 densities × 45 replicates = 810 vials (half with 30 eggs, the other half with 150 eggs per vial, for a total of 72900 eggs). The eggs were collected from the same cultures set up to measure fertility, so that the five strain combinations for each of the nine mating types were equally represented in each experimental block, except that the low-density and high-density experiments were done at different times.

(v) *Equilibrium frequencies and stability conditions*

These were determined according to the analytical and the numerical methods described by Moya & Ayala (1989).

3. Results

The fertilities of the nine mating types are given in Table 1. The values given are the average numbers of eggs laid by three females for 14 h (7 h in each of 2 days). A two-way analysis of variance indicates that female genotype has a significant effect on fertility, but male genotype does not; the interaction between the two is also significant (Table 2). The data for the different strains of a given *Sod* genotype have been combined in the error term of Table 2, since a preliminary analysis of variance had shown no significant strain effect.

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Table 1. *Fertility (mean number of eggs with standard error) of the nine mating types. The number of replicates is 20 for each mating type*

Female genotype	Male genotype *F/F*	*F/S*	*S/S*	Female average
F/F	92·5 ± 8·7	122·8 ± 10·4	147·6 ± 13·5	121·0 ± 2·9
F/S	179·8 ± 10·2	140·6 ± 9·9	138·8 ± 8·3	153·0 ± 2·4
S/S	120·4 ± 8·4	85·6 ± 6·8	71·8 ± 8·2	92·6 ± 2·6
Male average	130·9 ± 4·7	116·3 ± 3·0	119·4 ± 4·4	122·2 ± 11·4

The data in Table 1 show strong overdominance for the female genotype: *t*-tests show that the heterozygous females are significantly more fecund than either of the two homozygotes ($P < 0{\cdot}001$ for both comparisons). In addition, the females homozygous for the allele most common in nature (*F/F*), are significantly more fecund on the average than the *S/S* females ($P < 0{\cdot}001$).

The significant male × female interaction reflects that fertility is an attribute of the mating type and is not predictable from the fertility of the parental genotypes. Indeed, as shown in Table 3, the deviations from the 'expected' fertilities are quite large. Specifically, the fertility of the mating types involving male and female parents homozygous for the same *Sod* allele is considerably reduced (−37·1 and −18·7 for $F/F \times F/F$ and $S/S \times S/S$ respectively), whereas the fertility of matings between genetically dissimilar homozygous parents is substantially enhanced (+29·4 and +21·2 for the two $F/F \times S/S$ combinations). This effect has been named 'alloprocoptic' selection (Serradilla 7 Ayala, 1983*a*, *b*).

The egg-to-adult viability results are given in Table 4 and the analysis of variance is shown in Table 5. Density has a large effect on viability. The probability of survival is nearly 50% greater at the lower density of 30 eggs/large-vial than at the higher density of 150 eggs/small-vial. The lower density was chosen so that there would be no competition for limiting resources among the developing larvae, whereas at the higher density competition occurs. There is no significant interaction between density and either female or male genotype (Table 5).

Table 2. *Two-way analysis of variance for the fertility data*

Source of variation	SS	D.F.	MS	*F*
Female genotype (F)	241·9	2	121·0	31·0***
Male genotype (M)	14·6	2	7·3	1·9
F × M	149·6	4	37·4	9·6***
Error	664·6	171	3·9	
Total	1070·5	179		

*** $P < 0{\cdot}001$.

Parental genotype has a significant effect on survival rate, but there is no significant interaction between male and female genotype (Table 5). The most conspicuous genotypic effect in Table 4 is the lower average viability of the progenies of *S/S* parents. The *S/S* females in particular yield progeny viability rates that are invariably lower than those of other female genotypes: the female averages are at both densities significantly lower for the *S/S* homozygotes than for the *F/F* homozygotes ($t = 6{\cdot}64$, $P < 0{\cdot}001$ and $t = 7{\cdot}57$, $P < 0{\cdot}001$ at low and high density, respectively; D.F. = 28) or the *F/S* heterozygotes ($t = 6{\cdot}93$, $P < 0{\cdot}001$ and $t = 3{\cdot}60$, $P < 0{\cdot}01$; D.F. = 28).

The data in Tables 1 and 4 can be combined by multiplying the fertility of each mating type by the survival probability of its progeny. The results are shown in Table 6, which gives the number of adult progeny expected for each mating type under the conditions of the experiment. The data show overdominance for the female genotype at both densities. The male genotypes do not show overdominance; rather, there is an apparent underdominance at high density, although the effect is small compared to the overdominance of the females. Male underdominance was observed by Serradilla & Ayala (1983*b*) in similar experiments with other loci of *D. melanogaster*.

There is evidence of alloprocoptic selection in Table 6, as shown in Table 7 by displaying the observed-minus-expected deviations. At either density, male and female parents homozygous for different alleles produce more progeny than expected, whereas parents

Table 3. *Observed-minus-expected fertility for the nine mating types*

Female genotype	Male genotype *F/F*	*F/S*	*S/S*
F/F	−37·1	+7·6	+29·4
F/S	+15·8	−5·0	−10·7
S/S	+21·2	−2·5	−18·7

The 'expected' fertility is obtained from the data in Table 1 by multiplying the corresponding female and male averages and dividing this product by the average of all genotypes.

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Table 4. *Egg-to-adult viability at two densities: 30 (low) and 150 (high) eggs per vial. The values given are the mean percent survival with the standard error based on 45 replications*

Density	Female genotype	Male genotype *F/F*	*F/S*	*S/S*	Female average
Low	*F/F*	90·0 ± 2·0	92·3 ± 2·0	92·3 ± 2·0	91·4 ± 0·3
	F/S	95·3 ± 1·7	92·3 ± 2·0	90·0 ± 1·7	92·6 ± 0·7
	S/S	83·3 ± 3·3	89·3 ± 2·3	80·7 ± 3·3	84·4 ± 1·1
	Male average	89·6 ± 1·6	91·3 ± 0·4	87·7 ± 1·6	89·5 ± 1·5
High	*F/F*	62·3 ± 2·2	70·5 ± 3·9	72·5 ± 2·5	68·5 ± 1·4
	F/S	78·3 ± 4·5	57·2 ± 2·5	54·5 ± 1·1	63·3 ± 3·3
	S/S	50·3 ± 3·3	55·1 ± 3·3	50·3 ± 3·6	51·9 ± 0·7
	Male average	63·6 ± 3·6	60·9 ± 2·2	59·1 ± 3·0	61·2 ± 3·4

Standard errors for the grand means are obtained from the average value of the nine mating types.

Table 5. *Three-way analysis of variance for egg-to-adult viability. The data have been arc-sine transformed*

Source of variation	SS	D.F.	MS	*F*
Female genotype (F)	230	2	115	3·76*
Male genotype (M)	20	2	10	0·34
Density (*D*)	1762	1	1762	57·58***
F × M	146	4	37	1·20
F × *D*	16	2	8	0·26
M × *D*	7	2	4	0·12
F × M × *D*	29	4	7	0·24
Error	2202	72	31	
Total	4414	89		

* $P < 0{\cdot}05$; *** $P < 0{\cdot}001$.

homozygous for the same allele produce few progeny than expected.

If we assume Mendelian segregation, it becomes possible to derive from Table 6 the change in gene frequency, due to fertility and viability differences. If the initial frequency is 0·5 for each allele, after one generation of selection the frequency of the *F* allele among the adult progeny becomes 0·529 at low density, and 0·549 at high density. Following the procedures developed by Moya & Ayala (1989) for fertility selection, it is possible to ascertain the expected equilibrium frequencies of the *F* and *S* alleles when both fertility and viability are taken into account. A stable polymorphic equilibrium is predicted at both densities, with the frequency of *F* being $P = 0{\cdot}641$ at the low density and $P = 0{\cdot}695$ at the high density (Fig. 1). These values are fairly similar to each other and also to the equilibrium frequency estimated by Moya & Ayala (1989) for the *Sod* locus in *D. melanogaster* when fertility only is taken into account, which is $P = 0{\cdot}628$. This result underlines that fertility selection is an important contributor to fitness and may very well be the most important one under a variety of conditions.

Table 6. *Expected productivity (fertility × viability) of each mating type*

Density	Female genotype	Male genotype *F/F*	*F/S*	*S/S*	Female average
Low	*F/F*	83·3	113·3	136·2	110·9
	F/S	171·3	129·8	124·9	142·0
	S/S	100·3	76·4	57·9	78·2
	Male average	118·3	106·5	106·3	110·4
High	*F/F*	57·6	86·6	107·0	83·7
	F/S	140·8	80·4	75·6	98·9
	S/S	60·6	47·2	36·1	48·0
	Male average	86·3	71·4	72·9	76·9

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Table 7. *Observed-minus-expected productivity for the nine mating types*

Female genotype	Male genotype *F/F*	*F/S*	*S/S*
F/F	−35·6	6·3	29·3
F/S	19·1	−7·2	−11·9
S/S	16·5	0·9	−17·4
F/F	−36·4	8·8	27·6
F/S	29·7	−11·5	−18·2
S/S	6·7	2·7	−9·4

The expected productivity is obtained from the data in Table 6 following the same procedure as for Table 3.

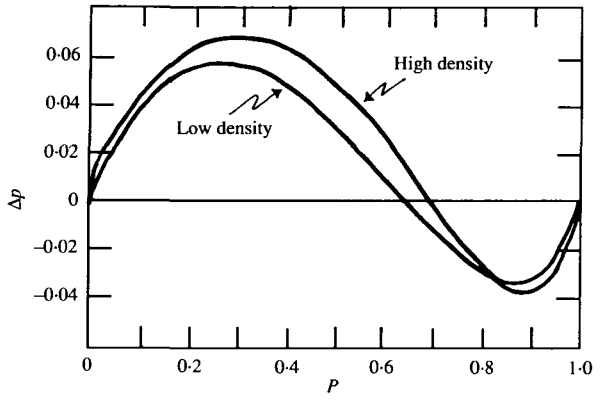

Fig. 1. Dynamics of allele frequency change at the *Sod* locus in *Drosophila melanogaster* when fertility and viability are both taken into account. The change, Δp, per generation for a given frequency, p, of the F allele is shown. A globally stable polymorphic equilibrium occurs at $P = 0{\cdot}641$ at low density, and at $p = 0{\cdot}695$ at high density. The observed frequency of F in the natural population sample is $p = 0{\cdot}873$.

4. Discussion

These experiments corroborate that fertility is a property of the mating type that cannot be predicted from the fertility of the genotypes of the female and male participating in the mating, i.e. fertility is not an additive property, as shown by the significant male × female interaction. Nor is fertility symmetric with respect to sex: reciprocal matings may have quite different fertilities (notice, e.g. in Table 1 that the fertility of ♀S/S × ♂F/S is $85{\cdot}6 \pm 6{\cdot}8$, whereas that of ♀F/S × ♂S/S is $138{\cdot}8 \pm 8{\cdot}3$, an increment of 62%). Our experiments show, in addition, that asymmetry and nonadditivity persist when survival rate to adulthood is taken into account (see Tables 6 and 7). But the fitness effects of mating type are considerably greater with respect to fertility than to viability.

The present experiments evidence alloprocoptic selection, a form of selection identified by Serradilla & Ayala (1983*a*, *b*), which is worth additional investigation because, if it turns out to be a common phenomenon rather than an oddity, it may be a significant contributor to the maintenance of genetic polymorphisms in nature. The magnitude of this effect in our experiment is considerable, as can be seen by noticing that the combined fertility of the two matings between similar homozygotes ($F/F \times F/F$ and $S/S \times S/S$) is 164·3, whereas the combined fertility of the two matings between the dissimilar homozygotes ($F/F \times S/S$) is 268·0, or 63% larger. This effect cannot be attributed to inbreeding, since all experimental flies carry two independently-sampled wild genomes (see Materials and Methods); and moreover the wild genomes carrying a particular *Sod* allele are unlikely to be related since the natural population is large (in the millions) and the frequency of the rarer allele (S) is substantial (0·127).

There is fertility overdominance among the females, but not among the males – a state of affairs that was also encountered by Serradilla & Ayala (1983*a*, *b*) with each of the three loci (*αGpdh*, *Adh* and *Acph*) of *D. melanogaster* investigated in their experiment. Heterozygote superiority is the most frequently invoked process for the maintenance of balanced polymorphisms in nature. In spite of some scepticism prevailing in years past, the evidence for overdominance at individual loci is gradually accumulating (see e.g. Peng, Moya & Ayala, submitted, for a recent example). Sved & Ayala (1970) and Seager, Ayala & Marks (1982) have moreover shown that heterosis over small chromosome segments is a pervasive phenomenon in laboratory populations of *Drosophila* (see also Prout, 1971; Sved, 1971; Mourão, Ayala & Anderson, 1972; Tracey & Ayala, 1974; Brittnacher, 1981).

Hadeler & Liberman (1975) were, to our knowledge, the first authors to remove the assumption of additivity from a model of fertility selection. Male × female interactions increase the complexity of mathematical models for the obvious reason that the number of mating types is the square of the number of genotypes, so that many more parameters are required for modelling selection. Previously published results, as well as the data herein presented, suggest that non-additivity is the rule rather than the exception with respect to fertility and, hence, that it must be incorporated in mathematical models as well as in the conceptual assumptions and theoretical considerations of natural selection (review in Moya & Ayala, 1989). The integration of fertility selection into population-genetic models of selection has significant theoretical consequences. The possible evolutionary outcomes are much more diverse than the outcomes possible when similar genetic assumptions are made for viability selection (Feldman & Liberman, 1985).

Little is known about the physiological processes that modulate the male × female fertility interactions. Current evidence indicates that at least two mechanisms are involved: (1) substances transmitted with the ejaculate during mating, and (2) olfactory cues, whether airborne pheromones or those transmitted by body contact. Although the specific genetic mechan-

isms determining the pheromones and other cues are unknown, there is good evidence that genetic variation exists with respect to factors that enhance or inhibit mating proclivity.

Gilbert *et al.* (1981) and Gromko *et al.* (1985) have shown in *D. melanogaster* that sperm replenishment obtained by repeated matings is correlated with female fecundity. Turner & Anderson (1983), found that repeated inseminations increase also the fecundity of *D. pseudoobscura* females. They hypothesized that this fecundity increase might be caused by nutrients transferred with the ejaculate, although other stimuli would be possible. Markov & Ankney (1984), have demonstrated the transfer of nutrients with the ejaculate in *D. mojavensis*.

The two cuticular hydrocarbons 7-tricosene and 7-pentacose are abundant in males, but not in females of *D. melanogaster*, although their abundance (particularly the ratio of one hydrocarbon to the other) varies extensively from strain to strain (Antony & Jallon, 1982; Jallon, 1984; van den Berg *et al.* 1984; Antony *et al.* 1985; Scott, 1986). These cuticular hydrocarbons function as antiaphrodisiacs: in particular 7-tricosene acquired by contact with other males decreases their rate of female courtship. The same effect takes place when synthetic 7-tricosene is topically applied to males (Scott, 1986; Scott *et al.* 1988). But these components also enhance female receptivity. Canton-S females, for example, mate more quickly with males from strains with high 7-tricosene levels than with males in which 7-tricosene is less abundant or nearly absent (Jallon, 1984).

Differences in 7-tricosene, 7-pentacose, and other male-predominant hydrocarbons may, therefore, affect male × female fertility interactions, in their function both as antiaphrodisiacs affecting other males and as mating stimulants increasing the receptivity of females. Scott & Richmond (1988) have shown that the expression of these hydrocarbons in males has a complex genetic basis, determined by X-linked loci as well as by at least two different sets of autosome genes.

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