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Adaptation to environmental heterogeneity in populations of *Drosophila melanogaster*

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Summary

For 29 generations, populations of *Drosophila melanogaster* were offered one favourable (standard) and one suboptimal (salt-supplemented) medium, either singly or simultaneously. Egg-to-adult viability, fecundity and choice of oviposition medium were measured at regular intervals on both resources up to 17 generations after initiation of the salt treatment. Except for a decrease in viability on salt medium in the single-resource populations (SRPs) maintained on the optimal medium, these fitness components remained unchanged. Estimation of a more inclusive measure of fitness, productivity, obtained at generations 27–29, revealed that: (1) the SRPs maintained on salt medium were more adapted to salt medium; (2) the mixed-resource populations (MRPs) were intermediate in their adaptation to salt medium between either type of single-resource population. These results support Levins' model of optimal strategy for populations living in a coarse-grained environment when the fitness set is convex. Family selection for increased and decreased resistance to salt in the medium, carried out for the viability component at generations nine and 19, showed that: (1) genetic variation with respect to this component was present in all populations; (2) the SRPs maintained on salt medium had responded to the salt treatment by eliminating sensitive genotypes; (3) in the first selection experiment, the MRPs had a greater amount of additive genetic variance with respect to viability than either type of SRP; in the second experiment, this difference was not significant, but it was in the predicted direction. The latter finding provides some evidence in favour of the hypothesis repeatedly presented in the literature that environmental heterogeneity could promote the maintenance of genetic variability in populations.

1. Introduction

The observation that most organisms live in variable environments has led to the question of how these organisms cope with environmental heterogeneity (Lewontin, 1957; Levins, 1962, 1963, 1968; Antonovics, 1971). Fitnesses can vary spatially as well as temporally owing to variation in the environment.

Levins (1962, 1963, 1968) presented several theoretical models of adaptation in response to different patterns of environmental variation. Some of the adaptations that can evolve are expressed at the level of the individuals, while others are expressed at the populational level. For the latter, Levins made several predictions concerning the optimal phenotypic composition of populations given the properties of the genetic system: in some cases polymorphism, in other cases monomorphism would be predicted.

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The thought that some of the genetic variation observed in natural populations may be correlated with environmental heterogeneity has been repeatedly expressed (Da Cunha, Burla & Dobzhanksy, 1950; Mather, 1955; Thoday & Boam, 1959; Van Valen, 1965; Antonovics, 1971; see also review by Hedrick, Ginevan & Ewing, 1976).

The experiments described below were intended to increase our understanding of the evolution in populations that are exposed to new and variable environments. More precisely, the particular case of a spatially heterogeneous environment was studied and compared to two constant environments in experimental populations of *Drosophila melanogaster*. In the variable-environment populations, two resources for feeding and ovipositing were offered simultaneously: one novel suboptimal medium and the standard favourable medium. Several fitness components and the relative amounts of genetic variation with respect to one of these components were measured in these populations and they were compared with those in two sets

of constant-environment populations, one being offered the suboptimal resource only, the other the favourable resource only.

2. Materials and Methods

(i) *Base population and derivation of the experimental populations*

All the experimental populations were initiated with flies from a population cage maintained in the laboratory since 2 August 1973. It was started with approximately 2200 F_1-progeny from crosses between 44 iso-female lines descended from females caught in South Amherst, Massachusetts, 'Markert site' in October 1971 by P. T. Ives' group. The lines had been maintained separately in the laboratory for two years in mass cultures in bottles on a medium of cornmeal, agar, killed yeast, corn syrup and malt, with propionic acid and ethanol to retard mould formation.

On 25 September 1975, the population was switched to an axenic medium modified from a recipe by David (1959) and David & Clavel (1965). Five percent sucrose was added to their mixture of cornmeal, agar and killed yeast, supplemented with a high concentration (0·5%) of methyl-*p*-hydroxybenzoate (Tegosept) in ethanol to completely suppress yeast growth and mould formation. This medium was chosen to prevent interference from possible adaptation of the live-yeast colonies to the low-fitness resource used in the experiment. The axenic medium was able to sustain as large a population as the cornmeal medium referred to above.

Twelve experimental populations were set up simultaneously from the base population in October–November 1975. Each population cage (36 × 24 × 16 cm) received approximately 2900 adults at initiation.

(ii) *The resources*

The favourable resource consisted of the standard axenic medium described above, and the suboptimal resource consisted of that same medium supplemented with sodium chloride to a final concentration of 3% (weight/volume of medium). High concentrations of NaCl in the medium reduce larval viability (Waddington, 1959; Miyoshi, 1961), lengthen the duration of the larval period, decrease female fecundity and reduce adult longevity (Miyoshi, 1961).

Preliminary experiments carried out in the absence of crowding indicated that the reduction of fitness on axenic medium supplemented with 3% NaCl as compared to standard axenic medium is as follows: egg-to-adult viability is decreased by 5–25%, fecundity is decreased by 62–87%, developmental time is 20% longer and survival of adults after 12 days is 25% compared to virtually 100% on standard medium. When females are given the choice between standard medium and salt-supplemented medium, 5–15% of all eggs are laid on salt medium. The lowering of female fecundity is due to the fact that salt medium is inadequate to stimulate egg production: females reared on salt medium but placed on standard medium at emergence are as fecund as females reared on standard medium and tested on standard medium.

(iii) *The experimental treatments*

Three types of populations were set up: (1) There were four single-resource populations (SRPs) with standard medium only. Two of these, IAa and IAb, were raised with 12 foodcups each (eight cups with 30 ml of medium and four cups with 10 ml of medium) and the other two, IBa and IBb, with four foodcups each (each cup containing 10 ml of medium). (2) There were two SRPs with salt-supplemented medium only, IIa and IIb, each provided with eight cups of 30 ml of salt medium. Lastly, there were six mixed-resource populations (MRPs) with standard and salt-supplemented media offered simultaneously. These populations, I IIa through I IIf, were provided with 12 cups each (eight cups with 30 ml of salt medium and four cups with 10 ml of standard medium).

From 4 December 1975, when the introduction of salt-supplemented medium into the SRPs-salt and the MRPs was begun, the schedule of cup renewal described in Table 1 was followed. Owing to the smaller amount of standard medium, the population size dropped to a very low number (a few hundred) in cages IBa and IBb. The population size also decreased considerably in cages IIa and IIb (to about 1000–2000) as a result of the presence of the salt medium. These low numbers continued throughout the experiment. Cages I IIa to I IIf always maintained larger populations (approximately 4000), somewhat smaller than the populations of IAa and IAb. Minimum generation time in the population cages was estimated to be 14 days on standard medium and 17 days on salt medium. All populations were maintained at 24 °C.

(iv) *Measurement of fitness components*

The populations were sampled at three-week intervals. Viability and fecundity were measured at each sampling and the tests for choice of oviposition medium were conducted at two-month intervals. All measurements were carried out in the absence of crowding and at 24 °C. Details of the procedures are given in Verdonck (1978). Because some populations were exposed to the two resources simultaneously, it was necessary when taking egg samples to use both resources in order to obtain a representative sample of adults for each population. The flies that hatched from each kind of egg sample were then tested on both resources.

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Table 1. *Rate of foodcup replacement in the experimental populations*

	Number of fresh foodcups introduced each fourth day			
	Standard medium		Salt medium	Number of days the cups remained in the cages
Populations	30 ml	10 ml	30 ml	
IAa, IAb	2	1	—	16
IBa, IBb	—	1	—	16
IIa, IIb	—	—	2	20
I IIa, b, c, d, e, f	—	1	—	16
	—	—	2	20

(v) *Measurement of the relative amounts of genetic variation for egg-to-adult viability*

A family-selection experiment was designed in which only those families with the highest and those with lowest resistance to salt were allowed to breed.

Egg samples were taken with standard medium. Twenty pairs of newly emerged adults were placed in bottles, one pair to a bottle, with a spoon with standard medium. The spoons were renewed every 24 h. The eggs were transferred to vials with standard medium and to vials with salt medium on alternate days until an adequate sample had been transferred. Progeny emerging from the vials were counted and the percentage survival on both media was computed. A resistance value (R) was obtained by taking the ratio: (% survival on salt medium)/(% survival on standard medium) for each family. From the 16 that produced the highest number of eggs, the four families that exhibited the lowest resistance and the four families that exhibited the highest resistance were kept as parents for the next generation. From each selected family, five pairs of flies were taken, mated according to a rotational mating scheme and placed in bottles with a spoon with standard medium. Thus, the four families with the lowest resistance gave rise to 20 new pairs that represented the L (low) lines. Similarly, the four families with the highest resistance gave rise to 20 H (high) lines. The procedure for egg laying and egg transfer followed during the first generation was repeated for the L and H lines. At the end of the second generation, resistance values were computed for all lines.

(vi) *Productivity measurements*

Productivity was measured on salt medium and on standard medium. Egg samples were obtained with standard medium. Between 18 and 24 pairs of flies were tested per type of medium per population at each measurement. Each pair was placed in a vial with the appropriate medium within a few hours of emergence. The pairs were transferred to fresh vials every 24 h. All vials through day 7 were kept and the resulting offspring counted. For each population the average number of live offspring produced per pair was computed for the salt and the standard medium.

(vii) *Longevity of adults*

The adults used in the productivity measurements were transferred to fresh vials until day 9. The number of dead adults was recorded daily during the productivity measurements and thereafter through day 10.

3. Results

Egg-to-adult viability was measured ten times over a period during which 21 generations elapsed on standard medium or 17 generations on salt medium. Throughout this period, survival on standard medium remained unchanged in all populations. Survival on salt medium declined somewhat in the four populations that were maintained on standard medium (IAa, IAb, IBa and IBb), but no change in survival on salt medium was apparent in the salt populations, IIa and IIb, nor in the six populations maintained on the mixed resources. A plot of resistance to salt against time showed a downward trend in populations IAa, IAb, IBa and IBb. In all instances the slope of the regression line was negative, although significantly so ($P < 0{\cdot}05$) in only three out of the eight cases. The non-significant probabilities tended to be low, however. Fisher's method for combining probabilities of independent tests (Fisher, 1958), gave a combined probability of $0{\cdot}05 < P < 0{\cdot}10$ for the four regressions involving the egg samples taken with standard medium and $P < 0{\cdot}005$ for the four regressions involving the egg samples taken with salt medium. Tables and graphs detailing the results of the viability measurements and of the fecundity and choice of oviposition experiments mentioned below, are given in Verdonck (1978).

Fecundity was measured nine times over a period

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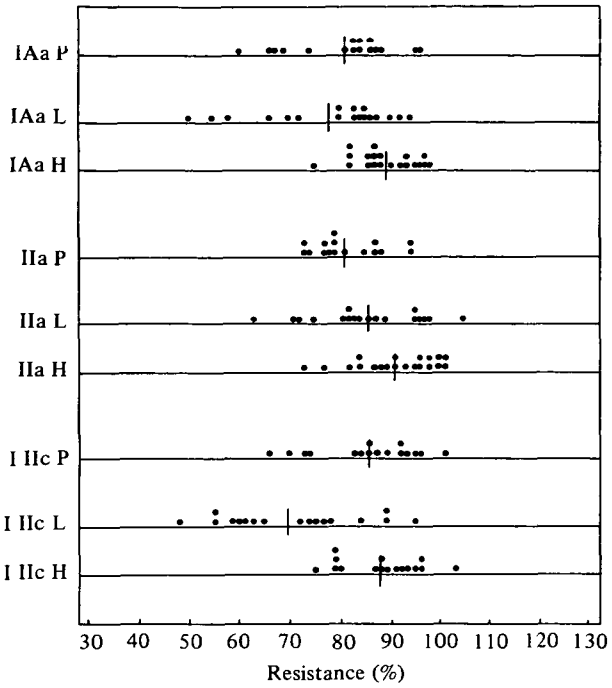

Fig. 1. Family selection for increased and decreased resistance to salt for egg-to-adult viability in populations IAa, IIa and I IIc. Distribution of resistance values for each family of the parental (P) and the selected (H and L) generations. Resistance is expressed as percentage and calculated as the ratio of viability on salt medium to viability on standard medium. Vertical bars indicate the mean for each distribution.

during which 19 generations elapsed on standard medium or 16 generations on salt medium. The choice of oviposition experiments were carried out after zero, four, seven and 14 generations of exposure to salt medium. No change in these fitness components was observed in any of these populations.

The family selection for increased and decreased resistance to salt was carried out with populations IAa, IIa and I IIc after nine generations, and with populations IAb, IIb and I IId after 19 generations on salt medium.

The results of this experiment are graphically shown in Figs. 1 and 2. Table 2 lists mean resistance, sample size and variance for the parental and for each of the L and H lines of the six populations tested. Given is also the difference in mean resistance $(\bar{R}_H - \bar{R}_L)$ between the H and L lines for each of the populations together with their one-sided probabilities obtained by carrying out a two-sample t test. In all the populations mean resistance is lower in the L line than in the H line and significantly so in four of the six cases. This indicates that after one generation, selection was able to produce a divergence between the lines selected for high and those selected for low resistance. This observation permits the important conclusion that there was genetic variation present in the populations with respect to egg-to-adult viability on salt medium. Thus, the absence of a measurable change in this fitness component as described above cannot be attributed to a lack of genetic variation for this character in the experimental populations.

The variances of the H and L lines are much larger in the second experiment than in the first experiment, possibly owing to technical problems that arose during the preparation of the medium in the second experiment. This may have contributed to the lack of statistical significance in two of the six comparisons.

The distribution of the resistance values in the SRPs on salt medium is characterized by the absence of low values, i.e. of *sensitive phenotypes*. Even in the second generation, where assortative mating between sensitive phenotypes occurred, phenotypes as sensitive as those present in the SRPs on standard medium and in the MRPs were not produced. This result indicates that selection for increased fitness on salt medium has eliminated sensitive genotypes from the SRPs on salt medium but has not produced more resistant genotypes.

The response to selection $(\bar{R}_H - \bar{R}_L)$ in the family-selection experiment is greatest in the MRPs. A t test to compare the response to selection in the MRPs with the response in the SRPs on standard medium and the SRPs on salt medium, produced the one-side probabilities indicated at the bottom of Table 2. The difference is highly significant in the first experiment but not in the second.

The productivity measurements were carried out after 27 and again after 29 generations had elapsed on salt medium in the experimental populations. Seven populations were tested: IAa and IAb, IIa and IIb,

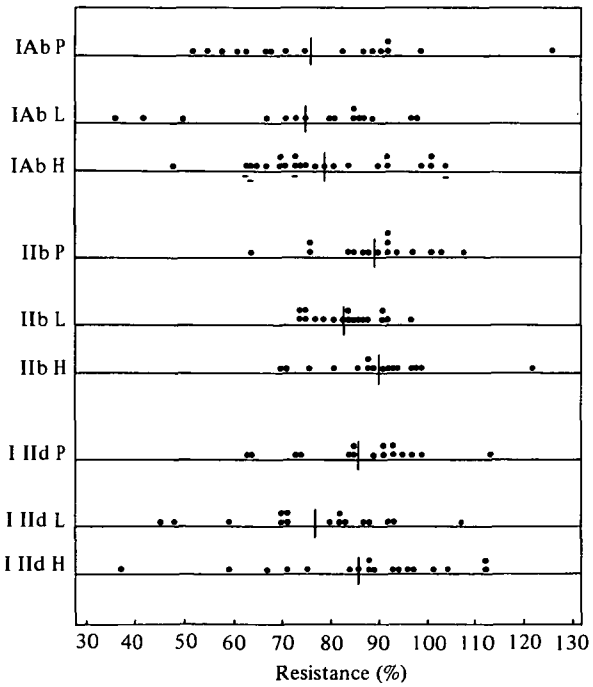

Fig. 2. Family selection for increased and decreased resistance to salt for egg-to-adult viability in populations IAb, IIb and I IId. Same method of plotting as in Fig. 1. See footnote *b* of Table 2 for additional explanations.

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Table 2. *Family selection for increased and decreased resistance to salt for the viability component*[a]

	$\bar{R}$	N	s^2		$\bar{R}$	H	s^2
(1) SRPs standard medium							
IAa P	80·74	16	107·94	IAb P	78·19	17	377·06
					75·19[b]	16	239·18
IAa L	77·78	18	168·02	IAb L	75·12	16	329·73
IAa H	89·09	20	30·70	IAb H	78·88	24	199·69
					79·41[b]	20	180·88
$\bar{R}_H - \bar{R}_L$	11·31	$0{\cdot}001 < P < 0{\cdot}005$		$\bar{R}_H - \bar{R}_L$	3·76	$P \simeq 0{\cdot}23$	
					4·29[b]	$P \simeq 0{\cdot}21$	
(2) SRPs salt medium							
IIa P	81·47	16	47·62	IIb P	89·46	16	119·84
IIa L	85·65	18	121·03	IIb L	83·42	18	47·74
IIa H	91·26	20	68·06	IIb H	89·67	16	153·51
$\bar{R}_H - \bar{R}_L$	5·61	$0{\cdot}025 < P < 0{\cdot}05$		$\bar{R}_H - \bar{R}_L$	6·25	$0{\cdot}025 < P < 0{\cdot}05$	
(3) MRPs							
I IIc P	85·59	16	102·30	I IId P	86·22	16	144·24
I IIc L	70·45	17	186·59	I IId L	76·70	16	272·24
I IIc H	88·15	16	62·00	I IId H	86·23	18	361·76
$\bar{R}_H - \bar{R}_L$	17·70	$P < 0{\cdot}001$		$\bar{R}_H - \bar{R}_L$	9·53	$0{\cdot}05 < P < 0{\cdot}10$	
IAa and IIa vs. I IIc: $0{\cdot}001 < P < 0{\cdot}025$							
IAb[c] and IIb vs. I IId: $P \simeq 0{\cdot}25$							

[a] Mean resistance ($\bar{R}$) expressed in percentage as defined in the text, with sample size (N) and variance (s^2) for the parental (P) and the selected lines (L, H). $\bar{R}_H - \bar{R}_L$, difference in mean resistance between H and L lines with their one-sided probability obtained in two-sample t tests. The bottom part of the table gives the one-sided probabilities obtained in two-sample t tests comparing the magnitude of the response to selection in the SRPs vs. the MRPs.

[b] Resistance, sample sizes and variances calculated omitting the family and its descendants that produced an unusually high R (= 126·16%) in the parental generation. (See Fig. 2: the descendants have been marked by a short line under the dots that indicate their location on the IAb H axis.) This high R was arrived at by an unusually low survival on standard medium (33·33%) and a low, but not unusually low, survival on salt medium (42·05%).

[c] Includes all families.

I IIc, I IId and I IIe. Table 3 shows the average productivities with their standard error. An analysis of variance of the results was carried out using the GLM procedure of the SAS computer system. The results of the combined analysis over both media tested, after logarithmic transformation of the observations, are presented in Tables 4 and 5. The analysis of Table 4 indicates a significant difference between productivities on standard and salt medium ($P = 0{\cdot}0002$). Similarly, at the treatment level, i.e. among the three types of populations, there is significant heterogeneity in productivity ($P = 0{\cdot}0115$). None of the other levels and interactions tested in the analysis of variance are significant. The medium-by-treatment interaction is close to significance and probably reflects a response to the selection. The analysis of Table 5 was obtained by using contrasts. It shows where the heterogeneity at the treatment level resides. The populations maintained on standard medium have a lower productivity on salt medium than those maintained on salt medium and those maintained on both media. The populations maintained on salt medium have a higher productivity on salt medium than those maintained on both media.

In addition to providing productivity comparisons, these experiments also yielded information on the longevity of adults. Virtually all adults kept on standard medium survived the test period and during this time there were no detectable differences in survivorship among flies from the different populations. Fig. 3 shows the proportion of adults surviving on salt medium during the first ten days of life and Table 6 compares the percentage of flies that are still alive at the end of day 10. Data for replicate populations (except for females from IIa and IIb) and replicate measurements were pooled for the statistical computations, after ascertaining that no heterogeneity existed among replicates. Pairwise comparisons were made using the normal approximation for comparison of binomial proportions. Adults from the SRPs on salt medium and the MRPs lived longer than adults from the SRPs on standard medium, except for females

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Table 3. *Productivity of the populations on standard and salt medium*[a]

Populations	Standard medium $\bar{P}\pm$S.E.$_{\bar{p}}$	*n*	Salt medium $\bar{P}\pm$S.E.$_{\bar{p}}$	*n*
(1) First measurement				
IAa	157·52 ± 12·40	19	7·23 ± 1·47	21
IAb	122·95 ± 13·16	20	11·80 ± 2·22	21
IIa	152·83 ± 18·63	18	30·36 ± 3·09	19
IIb	164·00 ± 11·79	23	25·73 ± 3·37	19
I IIc	143·22 ± 13·72	22	14·26 ± 2·41	19
I IId	112·73 ± 10·17	19	19·15 ± 2·52	19
I IIe	109·61 ± 12·44	21	15·80 ± 2·64	21
Second measurement				
IAa	125·23 ± 9·32	21	7·45 ± 1·73	20
IAb	130·42 ± 10·95	24	9·42 ± 1·94	19
IIa	114·52 ± 14·57	23	30·61 ± 3·55	21
IIb	148·27 ± 10·04	22	30·09 ± 3·23	21
I IIc	105·80 ± 12·69	21	15·75 ± 2·67	20
I IId	126·47 ± 12·34	19	20·05 ± 4·22	18
I IIe	109·79 ± 11·68	24	24·05 ± 2·92	19

[a] Productivity is expressed as the number of live offspring produced per pair during the first seven days of life. $\bar{P}\pm$S.E.$_{\bar{p}}$, average productivity ± standard error of *P*; *n*, number of pairs tested.

from IIb. Adults from the SRPs on salt medium, except for females from IIa, do not differ in their proportion surviving at day 10 from adults from the MRPs. Females from IIa lived longer than females from IIb. The latter apparently had a mode of adaptation different from that of females from IIa. However, there ostensibly was some response compared to females from IAa and IAb. In IIb the first female died at day 5, whereas in IAa and IAb the first females to die were two and three days old, respectively.

The flies from IIb had the same high average productivity on salt medium (during the first seven days of life) as the flies from IIa (Table 3). The survival patterns of the adult females in the two populations became different from day 5 onwards. The average productivities during the last two-day period (days 6 and 7) were not different in both populations. The results indicate that the increase of the lifespan on salt medium of the IIa females did not entail an increase in the number of offspring produced on that medium. An increase in progeny numbers could be caused by increased fecundity of the females and/or by increased egg-to-adult viability of the offspring, also by increased tolerance of the males to the salt.

Fig. 3 indicates that the males are consistently more salt-tolerant than the females of their respective populations. Males may be less susceptible to the toxic influence of salt since they are not involved in the production of eggs and hence they do not have to use the same quantity of medium as the females. On the other hand, it is not known what effects the salt might have had on male mating ability and fertility, hence on productivity.

4. Discussion

Of the four components of fitness that were measured only longevity of adults showed a clear-cut response to selection. An increase in viability and fecundity on salt medium had been expected, as well as a modification of the oviposition preferences of the females, in the SRPs on salt medium and in the MRPs. Whatever may have caused the unexpected decrease in viability on salt medium in all four SRPs maintained on standard medium, the behaviour of all salt-exposed populations was consistently different from the populations that were not exposed to salt medium.

The productivity measurements, on the other hand, demonstrated that the overall fitness on salt medium was higher in the SRPs on salt medium and in the MRPs. Because productivity partly reflects viability, the observed differences in productivity may in part be due to an actual decrease of the viability on salt

Table 4. *Analysis of variance of the productivity measurements obtained on standard and salt medium*[a]

Source of variation	D.F.	M.S.	*F*	*P*
Medium	1	618·22	177·17	0·0002
Treatment	2	16·82	16·61	0·0115
Medium × treatment	2	19·81	5·68	0·0679
Medium × replicate populations within treatment	4	3·49	3·25	0·1400
Pairs within replicate populations within treatment × measurement time × medium	545	1·35		

[a] The observations were transformed to log $(x+1)$. The following comparisons, with their degrees of freedom, had a *P* value $> 0{\cdot}4$ in the ANOVA: replicate populations within treatment (4), measurement time (1), medium × measurement time (1), treatment × measurement time (2), medium × treatment × measurement time (2), measurement time × replicate populations within treatment (4), medium × measurement time × replicate populations within treatment (4).

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Table 5. *Analysis of the heterogeneity in productivity observed among the experimental treatments*[a]

Source of Variation	D.F.	M.S.	F	P
(1) Productivity on standard medium SRPs standard medium, SRPs salt medium and MRPs	2	0·86	0·383	$P > 0{\cdot}25$
(2) Productivity on salt medium SRPs standard medium, SRPs salt medium and MRPs	2	34·99	15·55	$0{\cdot}001 < P < 0{\cdot}005$
SRPs standard medium vs. SRPs salt medium and MRPs	1	59·93	26·62	$0{\cdot}001 < P < 0{\cdot}005$
SRPs salt medium vs. MRPs	1	15·48	6·88	$0{\cdot}025 < P < 0{\cdot}05$

[a] Error term used for testing was (replicate populations within treatment M.S. + medium × replicate populations within treatment M.S.)/2 with 6 D.F. as given by Satterthwaite's approximation.

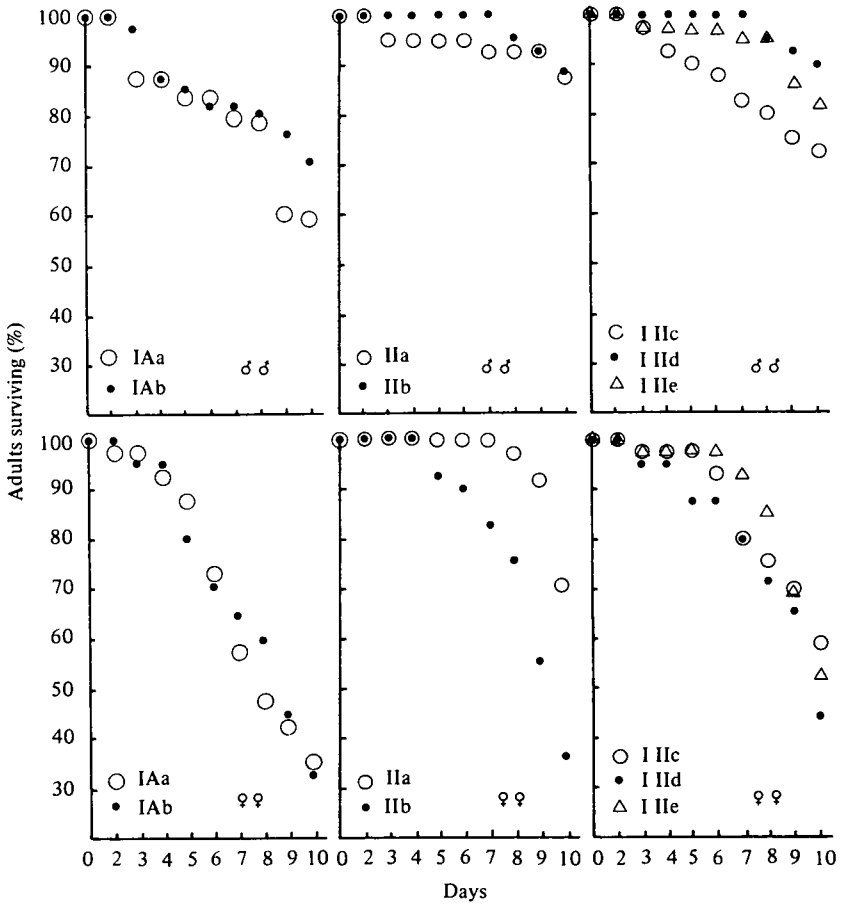

Fig. 3. Longevity of adults on salt medium. Percentage of adults surviving each day for the first ten days of life. See Table 6 for sample sizes. The data for the first and second measurements are pooled for each population.

medium in the flies from the SRPs on standard medium.

Levins' (1962, 1963, 1968) model and the fitness-maximizing strategies for populations derived from it, are based on the pattern of the environmental heterogeneity and the differential fitnesses of the phenotypes in the various subdivisions of the environment. The pattern of the environment in the MRPs of this experiment is coarse-grained (*sensu* Levins, 1968) for the larvae and fine-grained for the adults. The productivity measurements involved both larval and adult characters. According to Levins (1968) the strategy of

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Table 6. *Longevity of ♂♂ and ♀♀ on 3% salt medium*

♂♂		♀♀	
(1) Survival of adults at day 10[a]			
IA	64·86 (74)	IA	33·75 (80)
II	87·80 (82)	IIa	71·79 (39)
		IIb	36·84 (38)
I II	81·58 (114)	I II	51·72 (116)
(2) Pairwise comparisons of the survival of adults in the various population types[b]			
IA vs. II	$P = 0{\cdot}0006$	IA vs. IIa	$P = 0{\cdot}0004$
		IA vs. IIb	$P = 0{\cdot}7414$
IA vs. I II	$P = 0{\cdot}0096$	IA vs. I II	$P = 0{\cdot}0128$
II vs. I II	$P = 0{\cdot}2380$	IIa vs. I II	$P = 0{\cdot}0286$
		IIb vs. I II	$P = 0{\cdot}1096$
		IIa vs. IIb	$P = 0{\cdot}0020$

[a] Survival is expressed as percentage of adults still alive at day 10. The numbers within parentheses represent the numbers of adults tested for each type of population.

[b] For each comparison is given the two-sided probability obtained by testing the difference in percentage survival using the normal approximation for comparison of binomial proportions.

adaptation will be determined primarily by the immobile stages of the life-cycle. The fitness set with respect to resistance to salt was convex at initiation of the experiment and there is no indication that it became concave as a result of selection. In a coarse-grained environment, when the fitness set is convex, Levins predicts an 'ecological monomorphism' of the generalist type, a broad-niched population intermediate in its adaptation to the two environments. The results of the productivity measurements satisfy Levins' prediction for the particular environmental pattern under study. The MRPs are intermediate in their adaptation to salt medium when compared to both types of SRPs. The composition of the MRPs does not indicate the existence of specialists with respect to adaptation to salt: there are no more phenotypes with a resistance greater than 100% in the MRPs than in the SRPs (Figs. 1 and 2).

The productivity of the SRPs on salt medium (Table 3) indicates that those populations have not lost their adaptation to standard medium in becoming increasingly adapted to salt medium. This may mean that the productivity traits in the two environments are genetically correlated. The productivity measurements were not conducted in a way that such a correlation could be detected. The effect of a genetic correlation between traits selected in different environments, would be to limit the response of either trait to direct selection, and each trait may evolve to a locally optimum phenotype (Lande, 1980). The intermediacy of the adaptation to salt medium in the MRPs may in part be due to such a correlation.

The family-selection experiment provides some information about the way in which the populations responded genetically to the action of selection. Even though within- and between-generation comparisons indicate that the trait measured, i.e. egg-to-adult viability, is particularly sensitive to environmental effects, Figs. 1 and 2 show that the more sensitive genotypes have been eliminated in the SRPs on salt medium. Response to selection in these populations could be viewed as a shift in gene frequencies to extreme values, with an increase of genes conferring resistance. The MRPs, on the other hand, have retained sensitive genotypes and response to selection could be viewed as a shift of gene frequencies towards more intermediate values in these populations.

If environmental heterogeneity acts to maintain genetic variability, the MRPs should be genetically more variable than the SRPs, and one would predict a greater response to selection in the MRPs (Fisher, 1930; Falconer, 1960). The first family-selection experiment showed a statistically significant greater response in the MRP. In the second experiment, the difference in response between MRP and the SRPs was not statistically significant, but it was in the predicted direction. Even so, the parallel populations in both experiments, done ten generations apart, showed a similar pattern of the distribution of the resistance values (Figs. 1 and 2).

It is quite probable that maximum salt tolerance had not yet been attained in all salt-exposed populations by the time the experiment was terminated. Selection for increased salt tolerance was, and always would have been, weaker in the MRPs than in the SRPs on salt medium. Therefore, one would not expect the MRPs to attain the same level of adaptation to salt medium as the salt-SRPs once a plateau was reached. Even in the absence of a plateau in the experiment discussed here, the various populations evolved according to the predictions made by Levins' theory.

Some experimental evidence indicates the existence of a positive correlation between genetic variability and environmental heterogeneity in a number of animal species. Several studies have compared allele frequencies at protein loci (identifiable through electrophoresis) and environmental variables such as food, temperature, light, the presence of competitors: Powell (1971) studied *D. willistoni*; McDonald & Ayala (1974), Powell & Wistrand (1978), Powell & Taylor (1979) studied *D. pseudoobscura*. In contrast, Minawa & Birley (1975, 1978), Haley & Birley (1983) and Yamazaki *et al.* (1983) found no positive correlation between average genic heterozygosity and environmental heterogeneity in *D. melanogaster* populations. The study of quantitative characters requires a different experimental approach. Here too the evidence is conflicting. Beardmore (1961) and Beardmore & Levine (1963) found greater additive genetic variance of fifth sternite chaeta in *D. pseudoobscura* populations kept at diurnally fluctuating temperatures for 37 generations than in populations kept at constant temperature. Mackay (1980, 1981) found that spatially as

well as temporally varying environments maintained additive genetic variation for sternopleural bristle number and body weight, but not for abdominal chaeta number, in populations of *Drosophila melanogaster*. Additive genetic variance for female pupa weight in *Tribolium confusum* was not different in populations kept in a temporally varying environment from those kept in constant environments (Zirkle & Riddle, 1983).

The increase in additive genetic variance was not always reflected at the level of the phenotypic variance in the above studies: the latter almost always remained unchanged, even when the additive genetic variance increased. This suggests that perhaps populations may respond to variable environments by a redistribution of their environmental and various genetic variance components. Higher recombination rates and decreased dominance may result in greater additive genetic variance available to a population. Theoretical work has shown that fluctuating environments may favour increased recombination between some loci (Charlesworth, 1976), but that dominance modification will be only slightly affected although in the predicted direction, i.e. towards less dominance (Charlesworth & Charlesworth, 1979).

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