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Heterosis in crosses between lines of *Drosophila melanogaster* selected for adaptation to different environments

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Summary. Experiments were designed to examine whether heterosis would occur in crosses of *Drosophila melanogaster* populations adapted to 18 °C or 28 °C environments. Crosses were examined in parental environments, an intermediate environment (23 °C) and a mixed environment (alternating 18°/28 °C). Parental populations did not show divergence for larval viability, cold shock or high temperature mortalities when tested in a common environment. However, the 28 °C population was less fecund than the 18 °C population, but had higher larval competitive ability and higher adult longevity. Heterosis for viability, cold shock mortality and high temperature mortality occurred in crosses between a population adapted to 18 °C and another adapted to 28 °C, but not in crosses between two populations adapted to the same temperature. The results suggest that, in the absence of drift, heterosis is expected in crosses between lines or populations with different histories of selection but not between lines with the same selection histories.

Key words: Heterosis – Selection – *Drosophila* – Genotype × environment

Introduction

Heterosis will occur when two populations are crossed provided there is directional dominance and the populations are genetically different (Falconer 1981). It is usually assumed that the genetic divergence is due to random drift, but it could also be due to different selection pressures acting in the two populations. Frisch and Vercoe (1978) argue that the heterosis in crosses between Brahman cattle and British breeds occurs because these breeds have been subjected to different selection pressures in the past. For instance Brahman cattle have been selected for a lower maintenance requirement that British breeds, and the superiority of the crossbred occurs because an intermediate level of maintenance requirement is optimum for productivity in a harsh environment (Frisch and Vercoe 1978). This model implies epistatic gene action as well as dominance and much of the F1 heterosis should be maintained in the F2.

Populations maintained in a varying environment can be expected to have greater genetic variance and higher fitness than populations from a constant environment (Long 1970; Mackay 1981; Powell and Wistrand 1978). This suggests that heterozygote superiority is greatest in a fluctuating environment. Therefore, one might expect heterosis to occur in the cross of two populations adapted to different environments when the offspring are reared in a fluctuating environment.

If heterosis does occur in crosses between lines with different selection histories, this has important implications for livestock improvement concerning the choice of breeds for crossing and the design of breeding programs. It also has implications concerning the nature of genetic variation in natural populations. However, the experimental evidence on whether or not lines subject to different selection pressures without inbreeding show heterosis when crossed is scant and conflicting.

This report presents results of experiments conducted to examine whether heterosis would occur in crosses between lines of *Drosophila melanogaster* selected for adap-

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tion to 18 °C or 28 °C when compared in each of the parental environments, an intermediate environment (23 °C) and a mixed environment (alternating 18 °C and 28 °C). If heterosis were greatest in the 23 °C environment, this would support an epistatic model due to an intermediate optimum, whereas heterosis in a mixed environment could be explained by directional dominance for resistance to both temperature extremes.

Materials and methods

Experimental design

Four population cages were founded, each with 1000 or more adult *D. melanogaster* taken from a single cage population, and these were assigned to different temperature treatments. These treatments were 28 °C, 23 °C, 18 °C and an environment which alternated weekly between 18 °C and 28 °C. Two months after establishment a replicate cage population was founded from each of the original four so that, thereafter, there were two cages per treatment labelled A and B. The experiments reported here were conducted after the populations had had 16 months to adapt to their respective environments.

Table 1 presents the detailed experimental plan. Three crosses were made. The 18 °C population A by 28 °C population A cross ($18_A \times 28_A$) was made and raised in all test environments, to examine whether heterosis would occur in crosses between lines selected for different environments. Crosses between the two replicate cage populations maintained at 18 °C (18_A by 18_B) and 28 °C ($28_A \times 28_B$) were also made. Each of these two crosses were raised within an environment in which it was likely to display heterosis. Since Bell (1982) concluded that heterosis was greatest in a stressful environment, an adverse environment was chosen different from that to which their parental populations were adapted.

Daily, rather than weekly, alternating 18°/28 °C was used as the fluctuating test environment since most periods of measurement (e.g. for fecundity) were for less than 1 week.

Each genotype-environment cell in Table 1 comprised either six mating replicates for purebred genotypes or four mating replicates of each reciprocal cross. Each mating replicate contained three virgin females mated to three males in a vial.

Table 1. Schematic representation of the experimental plan; (×) represents genotypes studied within test environments

Genotype	Test environments			
	28 °C	Daily alternating 18°/28 °C	23 °C	18 °C
18A	×	×	×	×
18B	×			
23			×	
28A	×	×	×	×
28B		×		
18/28A*	×	×	×	×
18A × 28A	×	×	×	×
18A × 18B	×			
28A × 28B		×		

* Weekly alternating

Traits measured

For experimental purposes, adult flies were not removed directly from the cages; rather, populations were sampled by allowing flies to lay eggs for 24 h in fresh population vials. Larvae were then transferred into a 250 ml bottle containing 50 ml of media. Flies used for the experiments originated from the 250 ml bottle reared at 23 °C. Consequently, all population comparisons were made on flies developed under the same environment for a generation. This procedure also ensured that flies used in the experiments were of the same age.

Larvae to adult survival (larval viability) and adult fecundity (eggs laid per day) were measured as described by Ehiobu et al. (1988) for the combinations given in Table 1. Each mating replicate was used to setup one replicate of 25 first instar larvae (less than 12 h old) to measure larval viability. Flies emerging from this study were used to measure fecundity. Twenty replicates per purebred and ten per reciprocal cross of one male and one virgin female were used for each cell in Table 1. After mating for 48 h, egg production over the next 4 days was counted. The developing larvae and the adults during mating and egg laying in the alternating test environment were changed daily between 18 °C and 28 °C.

High and low temperature mortalities were measured only on flies reared in the 23 °C test environment. This procedure for cold shock treatment was as described by Ehiobu et al. (1988). Four replicates of 25 flies (two replicates of each sex) were used for each purebred and reciprocal cross genotype. After maturing for 2–3 days, flies were exposed to 1 °C for 48 h. The procedure for high temperature exposure was similar, but the treatment imposed was 37 °C at 100% relative humidity (above water bath) for 12 h. A recovery time of 1 h was allowed before mortalities were recorded.

Additional measurements

Two supplementary experiments were conducted to help define the genetic differences between the populations adapted to 18 °C and to 28 °C.

Competition study. The larval density in the cages at 28 °C was higher than in the other treatments, so competition between larvae was presumably more intense. However, in the test environments of the main experiment, larval densities were always low. Therefore, to determine whether the population from 28 °C was superior in a crowded 28 °C test environment, a study of competition against a stock of *D. melanogaster* carrying dominant markers *Cy*/*Pm* and *P1*/*P1* (*Cy* = In (2LR) SMI, *Pm* = In (2LR) bw VI and *P1* = In (3LR) H−41) was carried out. Virgin females from 18_A and 28_A cage populations and the marker stock were collected and mated to their respective males. Five replicates of (four female 18°A + eight female marker flies) and five replicates of (four female 28°A + eight female marker flies) were generated and allowed to oviposit on approximately 5 ml media for 24 h. Thereafter, the females were removed and vials containing the larvae and eggs were kept at 28 °C until emergence. Adults were collected for 3 consecutive days, separated into wild-type and markers and counted.

Longevity study. Longevity of 18_A and 28_A cage populations was studied in test environments of 18 °C and 28 °C. Three replicates of ten flies each for both sexes (females were virgins) were used for each cage population within each test environment. The flies, 14 h old at the start of the experiment, were transferred to fresh vials with feed every week. Mortality was recorded at 12 h intervals until all flies had died.

Table 2. Analysis of variance. Larval viability and adult fecundity

Effect	df	Larval viability		Fecundity	
		M.S.	F	M.S.	F
Strain	5	0.0294	1.08	476.0	3.53**
Maternal	3	0.018	0.66	120.0	0.08
Heterosis	3	0.4903	18.01***	1,913.33	14.20***
Test Environment	3	0.018	0.66	38,550.0	286.19***
Test Environment × Strain	6	0.02467	0.91	235.0	1.74
Test Environment × Heterosis	3	0.036	1.32	266.67	1.98
Error*		0.02722		134.7	
		(114)		(386)	

* Error degrees of freedom in parentheses
** ($P<0.01$)
*** ($P<0.001$)

Table 3. Analysis of variance. Cold shock and high temperature mortality

Effect	df	Cold shock mortality		High temperature mortality	
		M.S.	F	M.S.	F
Strain	3	0.0163	1.14	0.02773	2.55
Maternal	1	0.0013	0.08	0.0	0.0
Heterosis	1	0.182	11.74**	0.1337	12.30**
Sex	1	0.4643	29.95***	0.2215	20.38***
Error	17	0.0155		0.01087	

** ($P<0.01$)
*** ($P<0.001$)

Data analysis

Analyses of variance were done by least squares on the viability and fecundity data using the model:

$$Y_{ijklm} = \mu + S_i + S_j + M_j + Het_k + E_l + (S.E.)_{il} + (S.E.)_{jl} + (Het.E)_{kl} + e_{ijklm}$$

where

Y_{ijklm}	individual fecundity or larval viability for a cross between the i^{th} strain of sire and j^{th} strain of dam
μ	population mean
S_i and S_j	sire and dam strain effects (i, j = 1 ... 6)
M_j	maternal effect
Het_k	heterosis effect (k = 1 ... 4)
E_l	effect of the test environment (l = 1 ... 4)
$(S.E.)_{rl}$	strain by test environment interaction where r = i, j for paternal and maternal strains
$(Het.E)_{kl}$	heterosis by test environment interaction, and
e_{ijklm}	residual random error.

Cold shock and high temperature mortality were measured only on flies reared in a test environment of 23 °C and so no terms involving E were needed in the statistical model. The model used was

$$Y_{ijklm} = \mu + S_i + S_j + M_j + Het_k + Sex_l + e_{ijklm}$$

where

Y_{ijklm}	replicate cold shock or high temperature mortality
Sex_l	Sex effect (l = 1, 2), and

the remaining effects are as defined for viability and fecundity with i, j = 1 ... 4 and k = 1, 2.

The result of the longevity study were analysed using the model

$$Y_{ijklm} = \mu + S_i + E_j + (S.E)_{ij} + Sex_k + e_{ijklm}$$

where

Y_{ijklm}	average life in hours of the ten flies in a replicate vial
S_i	strain effect (1, 2)

and the other effects were as previously defined with j, k = 1, 2.

Results

Effect of strain and test environment

The analyses of variance are presented in Tables 2 and 3, and the larval viability and fecundity results are presented in Table 4.

Viabilities were generally very high in all test environments. Fecundity in all populations was high within 23 °C and 28 °C test environments, less for all populations in the daily alterning 18 °C/28 °C environment and least in the 18 °C test environment. There was a significant strain effect for fecundity because the 18_A strain had higher fecundity than the 28_A strain.

Table 4. Larval viability and fecundity

Lines	Test environments							
	28 °C		Alternating 18°/28 °C		23 °C		18 °C	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Larval viability (%)								
18_A	83.3	(2.4)	80.0	(5.4)	68.0	(6.6)	79.3	(4.3)
18_B	85.3	(2.5)						
23					84.7	(3.6)		
Alt 18/28	82.7	(6.2)	80.7	(3.5)	88.7	(3.3)	90.0	(2.3)
28_A	80.7	(4.1)	77.3	(6.1)	87.3	(3.2)	79.3	(2.7)
28_B			80.0	(5.4)				
$18_A \times 28_A$ *	90.5	(3.0)	95.5	(3.0)	97.0	(1.0)	95.0	(2.9)
$18^\circ_A \times 18^\circ_B$ *	83.0	(2.1)						
$28^\circ_A \times 28^\circ_B$ *			85.0	(2.6)				
Fecundity (eggs/day)								
18_A	88.0	(2.7)	64.9	(1.8)	79.1	(3.0)	36.0	(1.5)
18_B	79.9	(3.3)						
23					84.3	(2.3)		
Alt 18/28	80.0	(3.6)	65.7	(1.9)	84.8	(2.0)	39.6	(1.6)
28_A	78.6	(3.9)	57.3	(2.5)	77.5	(2.2)	32.4	(1.6)
28_B			67.0	(2.8)				
$18_A \times 28_A$ *	99.6	(2.8)	72.0	(1.9)	84.4	(2.0)	41.6	(1.7)
$18^\circ_A \times 18^\circ_B$ *	81.1	(4.3)						
$28^\circ_A \times 28^\circ_B$ *			61.2	(3.4)				

* Reciprocal crosses combined

Table 5. Cold shock and high temperature mortalities of populations and crosses raised in 23 °C test environment

Lines	Cold shock mortality (%)				High temperature mortality (%)			
	Male		Female		Male		Female	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
18_A	62.0	(6.8)	46.0	(7.0)	80.0	(5.6)	78.0	(5.7)
23	66.0	(6.6)	50.0	(6.3)	94.0	(3.3)	78.0	(5.9)
Alt 18/28	72.0	(6.3)	30.0	(6.4)	92.0	(3.8)	72.0	(6.3)
28_A	72.0	(6.3)	54.0	(6.9)	82.0	(5.4)	66.0	(6.7)
$18_A \times 28_A$ *	58.0	(6.7)	22.0	(5.8)	69.4	(6.5)	51.0	(7.1)

* Reciprocal crosses combined

Cold stress and high temperature mortality results are presented in Table 5. There was a tendency for 18_A flies to survive cold shock better than 28_A flies although it was not significant due to the large standard errors. High temperature mortality showed no definite trend among the populations. For both stresses, mortalities were higher among males than females.

The proportions of emergence of 18_A and 28_A flies tested in competition with marker flies at 28 °C, pooled over replicates, were $0.715 + 0.014$ and 0.790 ± 0.014 respectively. The difference between the two populations was significant ($P < 0.001$).

The mean longevities are presented in Table 6. The 28_A flies lived longer than the 18_A flies ($P < 0.06$). At 28 °C, flies had shortened longevity. Female 28_A flies tested at 28 °C had a mean longevity of 191 h which was within the peak egg production period of *D. melanogaster*. Females lived longer than males. No test of strain × environment interaction was significant (Table 7).

Heterosis

Heterosis estimates are presented in Table 8. For $18_A \times 18_B$ and $28_A \times 28_B$ crosses, estimates were close to

zero for both traits measured (viability and fecundity). However, the $18_A \times 28_A$ cross showed significant heterosis for all traits in all environments. The amount of heterosis for larval viability and fecundity was similar in the four test environments, as indicated by the lack of significant heterosis × test environment interactions in Table 2.

Table 6. Longevity of 18_A and 28_A strains. Mean longevity in hours for each sex and strain at each of two test environments

Strain	Sex	Test environment	Mean longevity ± S.E. (hours)
18	Male	18 °C	376.6±31.7
28	Male	18 °C	476.6±31.6
18	Female	18 °C	474.5±19.4
28	Female	18 °C	496.4±42.8
18	Male	28 °C	163.9±13.1
28	Male	28 °C	181.5±29.9
18	Female	28 °C	172.1±16.8
28	Female	28 °C	191.1±19.4

Table 7. Longevity of 18_A and 28_A strains. Analysis of variance for longevity

Effect	df	M.S.	F
Strain	1	9,420	4.07*
Test environment	1	466,750	201.88***
Strain × test environment	1	2,720	1.18
Sex	1	6,880	2.98*
Error	19	2,312	

* $(P < 0.1)$
*** $(P < 0.001)$

Discussion

Selection for adaptation to different temperature environments did not cause the populations to diverge significantly in larval viability, cold shock or high temperature mortality. However, they did diverge in fecundity, longevity and competitivness. The population adapted to 28 °C had a lower fecundity but higher longevity and competitiveness than the population from 18 °C. At 28 °C female flies lived for only 8 days, which is within the time of peak egg production. However, at 18 °C females lived for 20 days which is well after peak egg production. Therefore, one would expect more selection pressure for increased longevity at 28 °C than at 18 °C and this would explain why the 28_A flies live longer.

The index of competitiveness measured included fecundity and survival at 28 °C, but since the 28_A strain had lower fecundity and the same larval viability (under uncrowded conditions at 28 °C) as the 18_A strain, its superiority most likely occured during competition for resources during larval growth. The larval density is the 28_A cage vials was consistently higher than in the 18_A cage, so it is likely the populations at 28 °C were being selected for competitiveness.

The fact that the 18_A and 28_A strains displayed heterosis when crossed proves that they were genetically different. Divergence between the strains must have been due to the different selection pressures operating in the different environments, as the populations were initiated and maintained with over 1000 individuals, so drift can be ignored. That is, different alleles were favoured in the different environments or a genotype × environment interaction (G × E) existed for fitness.

Table 8. Heterosis* estimates

Test environment	Crosses							
	$18_A \times 28_A$				$18_A \times 18_B$		$28_A \times 28_B$	
	Fecundity ±S.E. (eggs/day)	Larval viability ±S.E. (%)	Cold shock mortality ±S.E. (%)	High temperature mortality ±S.E. (%)	Fecundity ±S.E. (eggs/day)	Larval viability ±S.E. (%)	Fecundity ±S.E. (eggs/day)	Larval viability ±S.E. (%)
28 °C	16.3±4.3 (19.6±5.1)	8.5±4.2 (10.4±5.1)			−2.7±4.3 (−3.2±5.1)	−1.3±4.2 (−1.6±5.0)		
Alt. 18°/ 28 °C	10.9±3.1 (17.9±5.0)	16.8±5.1 (21.4±6.5)					−0.9±3.0 (−1.5±4.8)	6.3±5.1 (8.1±6.5)
23 °C	6.1±2.9 (7.8±3.7)	19.3±4.4 (24.9±5.6)	−19.8±5.8 (−33.8±9.9)	−16.5±3.5 (−21.6±4.6)				
18 °C	7.4±2.0 (21.7±5.8)	15.7±5.4 (19.8±6.8)						

* Values in parentheses are heterosis estimates expressed as a percent of midparent values

However, no genotype × test environment interaction was found for the components of fitness larval viability and fecundity. There are two explanations for this: first, a G × E for fitness can occur without a G × E in its components. This could occur if one component, e.g. longevity, has a greater effect on fitness in the 28 °C environment than in the 18 °C environment. Secondly, the test environments may have differed in important respects from the cage environments. For instance, the high larval density may have been an important part of the 28 °C cage environment but all test environments had a constant low density.

Tantawy and Mallah (1961), working with temperate and tropical strains of *D. melanogaster*, found G × E's for body size and percent emergence, but only when a 30 °C environment was included. MacKay (1981) adapted *D.melanogaster* strains to environments with and without alcohol in the media, and tested both strains on both types of media. She found no G × E for bristle numbers and body size, but G × E for fitness was not examined.

Mourad (1965) and Anderson (1966) studied strains of *D. pseudoobscura* maintained for 4 years at 16 °C, 25 °C or 27 °C. Mourad (1965) found heterosis in crosses between strains from 16 °C and 27 °C, but he also found heterosis in crosses between strains from the same environment. Thus the genetic divergence between the strains could be due to drift rather than differential selection, despite the fact that the population size was large. Anderson (1966) found heterosis in body weight and development time in crosses 16 °C × 25 °C and 16 °C × 27 °C but not 25 °C × 27 °C. Both Mourad (1965) and Anderson (1966) found that most of the heterosis was lost in the F2 generation. Oliveira and Cordeiro (1980), working with *D. willistoni*, reported heterosis for productivity between strains adapted to high and normal pH media, and low and normal pH media when reared on normal media.

Bhuvanakumar et al. (1985) studied heterosis for growth rate amongst lines of mice selected for small or large 6-week weight and controls. The lines had an inbreeding coefficient of 0.6 so heterosis was expected in all crosses, but the heterosis was no greater in crosses between lines from different selection histories than between lines with the same selection history. In the same lines Bhuvanakumar et al. (1985) found the same result for reproduction, but Lynch et al. (1986) found some evidence for greater heterosis for traits associated with thermo-regulation in lines with different selection histories.

Since heterozygote superiority appears to be greatest in a fluctuating environment (Long 1970; MacKay 1981; Powell and Wistrand 1987), one would expect heterosis to be greatest in the alternating 18 °/28 °C environment. This did not occur for larval viability or fecundity but perhaps it would for total fitness, or perhaps the alternating test environment did not fluctuate in critical parameters such as larval density.

If heterosis is greatest in crosses where the parental lines have different selection histories, this should be taken into account when selecting livestock breeds for crossbreeding. It might also lead to different recommended breeding programs. For instance, it would provide an additional benefit for the use of specialised sire and dam lines selected for different traits. Kolstad (1980) selected lines of poultry for either a single trait (egg weight or egg number) or for an index of both traits. He found that the cross between the single-trait selection lines produced more eggs of a greater weight than the cross between two index selection lines. Liljedahl and Weyde (1980), working with poultry, and Wilhemson (1980), working with quail, did not find this superiority, but Liljedhl and Weyde (1980) did find greater heterosis in the cross of single-trait lines than in the cross of index lines.

Geneticists have long argued about the forces that maintain genetic variation. A simple neo-classical view would be that additive variation for metric traits is due to genes with additive effects on these traits but no effect on fitness, while heterosis is due to deleterious recessive genes held at a low frequency by a balance of mutation, selection and drift. This view is incompatible with our results, because selection would have little effect on the frequency of these deleterious recessives and, thus, would not lead to heterosis in crosses. An alternative view consistent with the results is as follows. Alleles affecting components of fitness such as fecundity occur at intermediate gene frequencies which can be altered by selection. Polymorphism is maintained because an allele which has a desirable effect on one component has an undesirable effect on another component of fitness. The desirable gene tends to be dominant for each component so that there is overdominance for fitness. Rose (1982) showed that such a model with antagonistic pleiotropy and dominance did maintain polymorphism and argued that experimental evidence supported it. In contrast, a model which involves dominance but not overdominance for fitness has difficulty explaining how the deleterious recessive allele is maintained in the population at a high enough frequency to contribute to the selection response.

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