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Heterosis in crosses between geographically separated populations of *Drosophila melanogaster*

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Summary. An experiment was performed to test the hypothesis that the genetic distance between populations estimated from enzyme loci could be used to predict the amount of heterosis that would occur in crosses between these populations. A partial diallel cross using 11 populations of *Drosophila melanogaster* from the Australian-Pacific region and from England was carried out. Heterosis for larval viability, fecundity, cold shock mortality, and an index of these three traits was recorded. When two populations originating from the same location were crossed, no heterosis occurred, but otherwise heterosis was significant for all traits. For larval viability, a similar low level of heterosis occurred in all crosses. For cold shock mortality, the level of heterosis varied widely and fecundity showed a pattern intermediate between these two. The geographic distance between the sites from which populations originated was not correlated with the amount of heterosis in their crosses. There was a tendency for populations from ecologically different environments to show heterosis in crosses. Genetic distance based on ten enzyme loci was correlated with heterosis for cold shock mortality and the combined trait index. These results can be explained by the hypothesis that genes affecting larval viability are subject to strong, uniform selection in all populations, which limits the extent to which gene frequencies can drift apart. However, genes affecting cold shock mortality and the enzyme loci are subject to different selection pressures in different environments. This divergent selection combined with genetic drift causes divergence in gene frequency and heterosis.

Key words: Heterosis – Genetic distance – *Drosophila*

Introduction

Utilizing heterosis is important in many farming systems. In most species of livestock, there are many breeds that could be used for crossbreeding, so many, in fact, that it is impossible to compare all possible breeds and crosses in field experiments. Therefore, it would be useful to be able to predict the heterosis that would occur in different crosses.

Provided there is no epistasis, heterosis depends on the difference in gene frequency between the populations or, equivalently, the increase in heterozygosity in the F_1. Goddard and Ahmed (1982) defined a statistic F' to measure this, where

$$F' = \frac{H_{F1} - H_P}{H_P}$$

H_P = mean heterozygosity of the parent breeds; H_{F1} = heterozygosity in the F_1.

If the populations have diverged due to genetic drift combined with migration, then the expected value of F' is the same for all types of loci. Consequently, gene frequencies at marker loci (e.g., enzyme loci) can be used to estimate F', which will be applicable to all loci including those causing heterosis.

Inbreeding depression is proportional to the inbreeding coefficient F, which may be written as

$$F = \frac{H_P - H_I}{H_P},$$

where H_P = heterozygosity of the parent population; H_I = heterozygosity of the inbred animals.

The depression in performance for a given increase in F should be the same as the increase in performance for the same increase in F'. Therefore, it should be possible to predict the heterosis expected in a particular cross by estimating F' from marker loci and estimating heterosis or inbreeding depression per percent F from inbreeding experiments.

If selection acts on some loci, then the expected value of F' will not be the same for all types of loci. For instance, if recessive genes which decrease viability are selected against in all populations, then less divergence of gene frequency will occur at these loci than expected from F' estimated from neutral markers. Although F' might still predict which crosses give the most heterosis, the level of heterosis would be less than expected from studies of inbreeding depression. If epistasis is important in causing heterosis, this might also reduce the relationship between F' and heterosis.

Empirical studies in pigs (Glodek 1974) and cattle (Goddard and Ahmed 1982; Graml and Pirchner 1984) have found that heterosis can be predicted to some degree from F' or other measures of genetic distance. However, it is very difficult with livestock to estimate heterosis accurately for a large number of crosses within a single experiment. Goddard and Ahmed (1982) and Graml and Pirchner (1984) combined data from many experiments, and this may affect the results obtained. Therefore, it was decided to study heterosis in crosses between populations of *Drosophila melanogaster* from different parts of the world. These populations are partially isolated, but exchange some migrants and are adapted to different environments. Most breeds of livestock also originated as local populations exchanging a limited number of migrants with other populations. Study of geographic variation in *Drosophila* has been an important topic in population genetics. Genetic differences in quantitative traits (Bouletreau-Merle et al. 1982), gene frequencies at electrophoretically defined loci (Singh and Rhomberg 1987), and of lethals (Yamazaki et al. 1986) and frequencies of chromosome rearrangements have been studied. Heterosis provides another measure of the genetic divergence between populations and so adds another dimension to this picture. It has the advantage that heterosis occurs most for traits closely related to natural fitness.

The experiment reported here uses 11 populations of *D. melanogaster* from different parts of the world. F' has been estimated from gene frequencies at ten electrophoretically defined loci, and heterosis has been estimated for larval viability, fecundity, and cold shock mortality.

Materials and methods

Populations and crosses studied

Drosophila melanogaster populations from Armidale, Brisbane, Cairns, Melbourne, Townsville, Darwin (Australia); Port Moresby (Papua New Guinea); Fiji; and Leeds (England) were used. These populations were each founded by at least 60 inseminated females trapped in the wild, and were maintained as large populations in the laboratory. [Further details of the fly populations were presented by Ehiobu (1985, p. 59).]

A partial diallel cross was carried out. The main experiment involved the eight Australian-Pacific populations and ten reciprocal crosses. The parent populations involved in each cross were classified for geographic distance (distance between their origins in km) and ecological distance (a subjective score based on similarity of climate).

A second experiment was conducted to extend the range of geographic distances involved by including crosses of populations from the same location (zero geographic distance) and crosses of the Leeds population with Australian ones. To this end, two Brisbane populations that originated from the same founder flies but separated at the time of establishment were used. A new Townsville population (Townsville II) was also established from 108 wild inseminated females caught 1½ years later at the same location as the first Townsville population. The Brisbane by Townsville cross of the main experiment was repeated to provide a link between the two experiments.

Mating

Three-day-old virgin females were mated to three males in a vial replicated four times for each reciprocal cross and six times for each straight-bred population.

Traits measured

Larval to adult survival (larval viability), adult fecundity (eggs laid per day), and adult cold shock mortality were measured as described by Ehiobu et al. (1989). Each mating replicate was used to set up 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. Ten replicates per reciprocal cross and 20 replicates per straight-bred of one male and one virgin female were used. After mating for 48 h, egg production over the next 4 days was counted. Flies used for the fecundity study were random samples of all viability replicates. Progeny of two mating replicates for each reciprocal cross and geographic population were used for the cold shock mortality study. A group of 25 males and a separate group of 25 females were obtained from each mating replicate. These groups were exposed to a temperature of 1 °C for 48 h and after a 1-hour recovery period, the number of dead flies was counted. To provide an overall measure of heterosis, an index combining the three traits was calculated by the formula

$$CTI = V/\sigma_V + F/\sigma_F - C/\sigma_C$$

where V = viability, F = fecundity, C = cold shock mortality, and each is divided by its standard deviation.

Data analysis

Least-squares analysis was carried out based on the model:

$$y_{ijl} = \mu + S_i + S_j + M_j + A_k + D_{ij} + e_{ijl}$$

where y_{ijl} = larval viability, fecundity, or cold shock mortality for the l^{th} replicate from the i^{th} sire population mated to the j^{th} dam population; μ = population mean; S_i and S_j = effect of sire and dam strains respectively ($i, j = 1 \ldots 8$); M_j = maternal effect of the j^{th} population; A_k = average heterosis effect ($k = l$ for purebred, $k = 2$ for crossbred); D_{ij} = heterosis in cross of strains i and j expressed as a deviation from average heterosis A_2; e_{ijl} = residual random error.

For the analysis of cold shock mortality, an effect of sex T_m ($m = 1, 2$) was added to the model. For the analysis of fecundity, a similar term was used to represent the effect of the time of day when the vials were changed.

Genetic distance estimation

All enzymes listed in Table 1 were assayed. Forty to fifty flies (equal numbers of males and females) were typed for each en-

zyme per geographic population. Third instar larvae were used for *Aph*. F' can be calculated from Wright's F_{ST} by the formula

$$F' = \frac{F_{ST}}{1+F_{ST}/2} .$$

F_{ST} was calculated correcting for sample size (i.e., the number of flies typed for each population) by

$$F_{ST} = \frac{\Sigma\,(\sigma_p^2 - \frac{1}{2}(S_x^2+S_y^2))}{\Sigma\,\bar{p}\,(1-\bar{p})}$$

where $\sigma_p^2=(p_x-p_y)^2/2$ is the variance of the allele frequency p between two lines X and Y, and p_x and p_y are the frequencies of the allele in lines X and Y. $\bar{p}=(p_x+p_y)/2$ is the average allele frequency. s_x^2 and s_y^2 are the sampling variances of the gene frequencies in lines X and Y. Σ indicates summation within and across loci.

Simulation study

The purpose of this simulation was to test whether a combination of migration and selection could explain some of the observed results.

A realistic model of population structure was mathematically intractable, so a simple island model was used. Decreasing migration rates represent increasing geographic distances.

In this model migration occurs from a large 'mainland' population to an 'island' with population $N_e=10{,}000$. There is a deleterious recessive gene with selection coefficient against the homozygote s and frequency on the mainland of 0.003. This model is mathematically equivalent to the mutation model of Crow and Kimura (1970, p. 445), and their formula for the distribution of gene frequency in a group of similar islands was used to calculate the F_{ST} value among these islands. Greater geographic distances and, consequently, lower migration rates were modelled by decreasing the migration rate from the 'mainland' to the 'island' from 10^{-2} to 10^{-8}. The calculations were done for selection coefficients (s) of 0.01, 0.1, and 0.9.

Results and discussion

Gene frequencies

Table 1 presents estimated gene frequencies for enzymes assayed. The Darwin population was polymorphic for all loci. *Xdh* was polymorphic only in the Darwin population. Consequently, the *Xdh* locus contributed little to genetic differentiation between the populations.

The mean gene frequencies reported here are in agreement with those reported by Anderson (1981) for *Pgm*, *6-Pgd*, *α-gpdh*, *Odh*, *Est-6*, and *Acph* loci. However, significant differences between gene frequencies reported here and those reported by Anderson (1981) and Oakeshott et al. (1982) were detected for some loci in some populations. For example, Adh^F frequency was estimated as 0.525 for the Darwin population in the present study, while Anderson (1981) and Oakeshott et al. (1982) obtained estimates of 0.34 and 0.09, respectively, for their Darwin populations. The differences between these results could be partly due to sampling error in all experiments. However, the most likely cause of the difference in gene frequency is that populations from a geographic location are not homogeneous. The Darwin population samples were obtained at different times (year/season) and from different sites. Franklin (1981) confirmed seasonal variation in gene frequencies of *Drosophila melanogaster*, with *Pgm* varying the most and *Acph* the least. Consequently, population samples collected at different times (year or season) could reflect different populations' gene frequencies.

Oakeshott et al. (1981, 1982, 1983a, b) found latitudinal clines in gene frequency at the *α-gpdh*, *Adh*, *Odh Acph*, *Est-6*, and *6-Pgd* loci. In our data the only significant correlation with latitude was the frequency of *α-gpdh* fast allele, which was most common in the tropics. However, the trend for other loci was similar to that observed by Oakeshott et al., and the lack of significance is not surprising given that we had only eight data points.

Geographic variation in gene frequency at these loci appears to be due in part to natural selection, since similar clines have been reported in North America, Europe, and Asia (Oakeshott et al. 1981, 1982, 1983a, b).

Table 1. Estimated population gene frequencies

Populations	Lat in °S[b]	Allelic frequencies											
		Pgm^F	Pgm^s	Pgm^{ss}	$6pgd^F$	Xdh^F	Adh^F	$gpdh^F$	Mdh^F	Odh^F	$Est\text{-}6^F$	$Acph^F$	Aph^F
Port Moresby	9.5	0.15	0.72	0.13	0.80	0.00	0.26	0.71	0.19	1.00	0.00	0.80	0.41
Darwin	12.5	0.21	0.77	0.02	0.84	0.07	0.53	0.63	0.16	0.79	0.46	0.99	0.14
Cairns	17.0	0.06	0.94	–	0.57	0.00	0.34	0.58	0.15	0.93	0.54	0.74	0.21
Fiji	17.0	–	1.00	–	0.85	0.00	0.76	0.80	0.06	1.00	0.30	0.99	0.39
Townsville	19.3	0.14	0.77	0.09	0.75	0.00	0.45	0.74	0.05	0.99	0.48	1.00	0.39
Brisbane	27.5	0.10	0.99	–	0.74	0.00	0.35	0.64	0.31	0.90	0.31	0.93	0.23
Armidale	30.5	–	1.00	–	0.92	0.00	0.61	0.39	0.00	1.00	0.38	0.88	0.10
Melbourne	36.4	0.02	0.88	0.10	0.92	0.00	0.60	0.11	0.14	1.00	0.43	0.98	0.15
Leeds	−54.0	0.24	0.63	0.13	0.92	0.00	0.55	0.75	0.13	1.00	0.23	0.99	0.16
Average[a]		0.09 (0.07)	0.86 (0.88)	0.05 (0.04)	0.81 (0.80)	0.01 (0.01)	0.50 (0.49)	0.59 (0.57)	0.13 (0.13)	0.96 (0.95)	0.35 (0.36)	0.92 (0.91)	0.24 (0.25)

[a] Average gene frequencies of Australasian populations in parentheses
[b] Negative values indicate °N

Distance measures

Geographic, ecological, and genetic distances between the populations crossed for the main experiment are presented in Table 2.

Tables 2 and 3 show that genetic distance tends to increase with both geographic and ecological distance. For instance, the genetic distances between Cairns–Townsville (low geographic distance) and Armidale–Melbourne (low ecological distance) are both small. In addition, barriers to migration such as the ocean and Australia's strict quarantine laws may be increasing distances such as Darwin–Port Moresby and Cairns–Fiji.

Table 2. Genetic, ecological, and geographic distances between crosses

Crosses[a]	Geographic distance (km)	Coded ecological distance[b]	Genetic distance ±SE
CT	300	1	0.05±0.03
AB	500	2	0.10±0.04
CPm	800	2	0.13±0.08
AM	1,100	1	0.05±0.03
BT	1,200	2	0.05±0.03
DPm	1,600	1	0.13±0.06
APm	2,200	3	0.19±0.06
BF	2,700	2	0.10±0.05
DM	2,900	2	0.11±0.07
CF	3,200	1	0.15±0.05
Average	1,650	1.7	0.11

[a] CT = Cairns × Townsville; AB = Armidale × Brisbane; CPm = Cairns × Port Moresby; AM = Armidale × Melbourne; BT = Brisbane × Townsville; DPm = Darwin × Port Moresby; APm = Armidale × Port Moresby; BF = Brisbane × Fiji; DM = Darwin × Melbourne; CF = Cairns × Fiji

[b] 1 = Similar climates; 2 = Moderately dissimilar climates; 3 = Extremely dissimilar climates

These three factors (geographic distance, ecology, and migration barriers) could explain the fact that the largest genetic distance is that between Armidale and Port Moresby.

Similar values of F_{ST} have been reported by Singh et al. (1982) and Singh and Rhomberg (1987). Singh and Rhomberg (1987) found that over all polymorphic loci, F_{ST} was 0.07 for *D. melanogaster* populations on the west coast of North America and 0.17 for world wide populations. Singh and Rhomberg (1987) and Yamazaki et al. (1986) found that genetic distance slowly increased as geographic distance increased from 0 to 10^4 km. The low genetic distances are due in part to the high migration rates. Singh and Rhomberg (1987) estimated the number of migrants per generation (Nm) to be in the range of 1.0 to 3.0.

Heterosis estimates

Heterosis estimates for each trait are presented in Table 4. Estimates of cold shock mortality heterosis are mostly negative because crossbreeds had lower mortality than purebreds. Crossbreeds were consistently better than purebreds for all traits. Consequently, average heterosis was always significant (Table 5).

Heterosis estimates differed between the traits. Larval viability showed low and consistent levels of heterosis, while those for fecundity were higher, but still not very variable between crosses. Cold stress mortality showed high levels of heterosis, and this varied widely between crosses so that this was the only trait for which deviations from average heterosis were significant (Table 5).

Over the range of geographic distances in the main experiment (500–3,000 km), there was no significant correlation of geographic distance with heterosis, although the trend is in the expected direction. The results

Table 3. Correlation matrix of distance measures and heterosis estimates for the geographic crosses

	Distances			Heterosis estimates		
	Geo	E	G	V	F	C
Distances						
Geographic (Geo)	–					
Ecological[a] (E)	0.31	–				
Genetic (G)	0.53	0.36	–			
Heterosis						
Larval viability (V)	0.04	0.29	0.15	–		
Fecundity (F)	0.25	0.62**	−0.21	0.23	–	
Cold shock mortality (c)	−0.09	−0.26	−0.61**	0.04	0.54	–
CTI	0.13	0.36	0.69*	0.26	−0.32	−0.93*

* ($P<0.05$)

** ($P<0.1$)

[a] Nonparametric rank correlation coefficient

of the supplementary experiment clarify the position somewhat. Populations from the same location show no heterosis in crosses, while crosses of the Leeds population with Australian populations show no more heterosis than crosses among Australian populations. Therefore, as geographic distance increases from zero, heterosis must increase but reach a plateau at distances of less than 1,000 km. Fecundity shows more heterosis than larval viability and may reach the plateau at a higher distance.

The simulation study helps to explain these results. Figure 1 shows how population differentiation (measured by F) changes with increasing geographic distance represented by decreasing migration rate. For each level of selection intensity, F increases with geographic distance until a plateau is reached. With a high selection coefficient, the plateau occurs at a lower geographic distance and at a lower level of F than when selection is weak.

It seems likely that average selection coefficients at loci affecting larval viability are higher than at loci affecting cold stress mortality, with fecundity perhaps intermediate between the two. At one extreme, viability will be affected by recessive lethal genes. Natural selection keeps these genes at low frequency except in very small populations. Wallace (1966) and Yamazaki et al. (1986) found that the allelism rate of lethal chromosomes in *D. melanogaster* decreased as the distance between populations increased, but a plateau was reached at less than 100 km. Therefore, heterosis caused by covering up lethals will not be large and will reach a plateau at a small geographic distance.

The levels of F found in the simulation study are lower than those observed for protein loci, and would not explain the levels of heterosis observed (see section on inbreeding depression and heterosis). This may imply that effective population sizes in real populations are less than that used for simulations or that selection coefficients vary from one population to another, but the principle illustrated by the simulation is still relevant.

Bonner (1960) also found a positive but nonsignificant correlation between fecundity heterosis and geographic distance in *D. melanogaster*. Moll et al. (1965) studied heterosis in crosses of inbred lines of corn derived

Table 4. Heterosis estimates for each trait in the geographic population crosses

Crosses[b]	Larval viability (%)	Fecundity (eggs/day)	Cold shock mortality[a] (%)	CTI
Main experiment				
AB	8.3	16.6	− 5.5	2.3
AM	8.2	13.6	−17.5	3.0
APm	7.5	16.7	−38.0	5.2
BF	5.2	20.6	− 1.5	2.1
BT	6.2	21.2	− 2.0	2.3
CF	5.3	14.3	−13.5	2.5
CPm	3.0	10.4	33.5	4.1
CT	−0.7	14.7	−10.5	1.8
DM	1.7	16.2	−21.5	2.9
DPm	5.0	12.5	−11.5	2.7
SE*	4.1	3.9	6.1	1.0
Supplementary experiment				
BB′[b]	4.2	−2.7	5.7	−0.7
TT′[b]	−1.8	2.1	− 1.6	0.3
BT	9.3	17.0	−11.6	4.1
LT	8.5	9.7	−10.8	3.3
LM	10.0	17.1	−15.2	4.4
SE*	4.2	4.3	3.0	1.7

* Standard error of each heterosis estimate
[a] Sexes combined
[b] BB′ and TT′ are crosses between the two Brisbane and Townsville populations, respectively; other abbreviations as in Table 2

Table 5. Analyses of variance of performance of geographic populations and their crosses

Effects	*df*	Larval viability		Fecundity		Cold shock mortality		CTI	
		M.S.	F	M.S.	F	M.S.	F	M.S.	F
Strain	7	0.028	0.97 n.s.	1,408	3.36***	0.151	7.84***	1.15	1.24 n.s.
Maternal	7	0.025	0.85 n.s.	360	1.36 n.s.	0.011	0.57 n.s.	0.81	0.87 n.s.
Av. heterosis	1	0.286	9.93	22,100	99.82	0.899	46.73***	44.30	47.79**
Between cross heterosis	9	0.015	0.54 n.s.	155	0.70 n.s.	0.115	5.99***	1.12	1.21 n.s.
Time	1			0	0.0 n.s.				
Sex	1					2.586	134.41***		
Error*		0.029		221		0.019		0.93	
		(103)		(360)		(86)		(3)	

* Values in parentheses are degrees of freedom
** ($P<0.01$)
*** ($P<0.001$)
n.s. Not significant

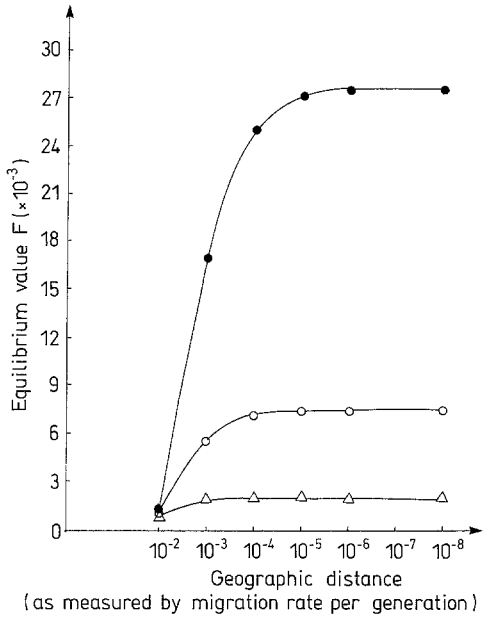

Fig. 1. Simulated relationship between equilibrium value of inbreeding coefficient (F) and migration rate under very weak selection, s = −0.01 (•); weak selection, s = −0.1 (○); and very strong selection, s = −0.9 (△)

from different locations. They found that heterosis initially increased with increasing geographic distance, but at high levels of distance heterosis decreased.

Ecological distance was more highly correlated with heterosis than was geographic distance, but the correlations were still not significant. It is possible that a more accurate measure of ecological distance, based on an index of climatic and environmental variables that most affect *Drosophila* populations, would be a better predictor of heterosis.

Genetic distance (F_{ST}) was significantly correlated with cold shock mortality and heterosis for the combined trait index, but not with heterosis for larval viability and fecundity. Evidence for a similar correlation has been found in pigs (Glodek 1974) and cattle (Goddard and Ahmed 1982; Graml and Pirchner 1984).

Heterosis and inbreeding depression

The theory concerning the prediction of heterosis presented by Goddard and Ahmed (1982) and in the 'Introduction' can be split into two parts. Firstly, is predicts that the lines or populations with the largest genetic distance (F_{ST}) between them will show the most heterosis when crossed. Secondly, it predicts that, if F' is estimated from neutral markers, then the heterosis per percent F' will be the same as the inbreeding depression per percent F. Table 6 compares the results of this experiment with those of two experiments on inbreeding. Ehiobu et al.

Table 6. Mean heterosis or inbreeding depression per percent F

	Larval viability (%) ±SE	Fecundity eggs/days ±SE	Cold shock mortality (%) ±SE
Inbreeding			
Full-sib (one generation)	0.96±0.22	1.11±0.21	−0.56±0.23
$N=4$	0.55±0.14	0.76±0.14	
$N=20$	0.42±0.17	0.84±0.19	
Crossbreeding			
Lines sib mated[a]	0.62±0.17	0.63±0.17	
For eight generations[b]	0.23±0.03	0.23±0.02	
Geographic populations	0.47±0.15	1.47±0.27	−1.46±0.30

[a] F calculated from marker loci
[b] F expected from eight generations of sibmating

(1989) compared inbreeding depression caused by three rates of inbreeding – full sib, $N=4$, and $N=20$. Ehiobu et al. (1990) measured heterosis in crosses between lines that had been inbred by sib mating for eight generations.

Table 6 shows that heterosis/percent F' for larval viability was only about half the inbreeding depression/percent F caused by sibmating. However, when inbreeding occurred over several generations so that selection also acted, the depression/percent F was also low. These results can be explained by the assumption that natural selection against genes that decrease larval viability occurs in all populations and, therefore, gene frequencies at these loci do not drift apart as would be expected for neutral genes. The lack of population differences in mean larval viability is consistent with this interpretation. This would also explain why heterosis for larval viability does not continue to increase as geographic distance or genetic distance increases above a threshold level. Goddard and Ahmed (1982) and Graml and Pirchner (1984) also found that for traits that might be subject to strong selection (fertility and milk yield) and where divergence between breeds occurred slowly (*Bos taurus* versus *Bos indicus*), the heterosis/percent F' was less than inbreeding depression/percent F.

For cold shock mortality, the heterosis/percent F is significantly more than the inbreeding depression/percent F caused by sib mating. This implies that divergent selection has caused the gene frequencies at loci affecting cold shock mortality to differ from one population to another. Consistent with this interpretation, there are significant differences between populations in this trait. Ehiobu and Goddard (1989) demonstrated that heterosis occurred in crosses between populations that had been exposed to different selection pressures for many generations.

Conclusions

The results could be explained by the following hypotheses.

The extent to which populations of *D. melanogaster* have diverged genetically depends on the type of loci considered. Genes affecting larval viability appear to be subject to strong, uniform selection in all populations, so that genetic drift can cause only a limited amount of divergence. Consequently, as we increase the distance and degree of isolation between populations, the genetic divergence and hence the heterosis in crosses soon reach an upper limit.

Conversely, genes affecting cold shock mortality appear to be subjected to different selection pressures in different populations. Therefore, populations diverge more in gene frequency than would be expected from genetic drift, and considerable heterosis occurs in crosses, especially between populations from different environments.

Gene frequencies at enzyme loci drift apart and for some loci are drawn apart by divergent selection pressures. Consequently, genetic distance based on enzyme loci will predict heterosis best for traits that are subject to a similar pattern of drift and divergent selection. This appears to be the case for cold shock mortality.

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