Temporal and spatial distribution of phosphoglucomutase (PGM) polymorphism in natural populations of *Drosophila melanogaster*

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Summary. Drosophila melanogaster adults were collected for several years in various localities of Italy. The frequencies of the *Pgm* electrophoretic alleles were determined and the similarity of the configuration of allelic frequencies observed. It was concluded that the PGM electrophoretic polymorphism could be maintained by random genetic drift in the natural populations studied only if the effective breeding size (N_e) during the bottle-neck period is about 5000.

The long-standing debate between panselectionists and panneutralists is still far from being exhausted[2-5]. Only a direct approach would permit the evaluation of the importance of the two main factors of microevolution (selection and random genetic drift) in the maintenance of genetic variations, but this is not feasible in practice. It is therefore necessary to resort to the indirect approach, e.g. to look for the expected consequences of a prolonged action of selection. The tests involved are usually based on the idea that any spatial (i.e. between populations) or temporal (i.e. between different generations in the same population) pattern of gene frequencies not compatible with chance alone would suggest selection.

The criterion adopted here consists of comparing the allele frequency patterns of a structural gene in consecutive years in different natural populations subjected every year to the bottle-neck effect. This is to see whether or not the variations observed depend on genetic drift alone. The phosphoglucomutase locus ($Pgm = 3:43.6$)[6] and *Drosophila melanogaster* have been chosen for this test. The *Pgm* locus is polymorphic for 2 common electrophoretic alleles, $Pgm^{1.00}$ and $Pgm^{0.70}$. There have also been 5 rare electrophoretic alleles[7] described so far $Pgm^{0.55}$, $Pgm^{0.85}$, $Pgm^{1.10}$, $Pgm^{1.20}$ and $Pgm^{1.50}$. Moreover, heat denaturation studies have shown that still more genetic heterogeneity exists at this locus, there being 2 heat-sensitivity polymorphic alleles within the electrophoretic $Pgm^{1.00}$ allele, whereas the $Pgm^{0.70}$ common allele consists of only a homogeneous heat sensitive class[8], $Pgm^{0.70,ts}$.

In this paper the gene frequencies of only the *Pgm* electro-

Allelic frequencies at the *Pgm* locus of 12 natural populations* of *Drosophila melanogaster* collected in consecutive years**

Locality	Years of collection	Genes sampled	*Pgm* electrophoretic alleles		
			$Pgm^{1.00}$	$Pgm^{0.70} \pm$ SE	Rare***
Veneto: Mareno	1977	456	0.923	0.057 ± 0.011	0.020
	1978	271	0.926	0.074 ± 0.016	-
Umbria: Perugia	1976	142	0.915	0.085 ± 0.023	-
Latium: Nazzano	1970	660	0.912	0.088 ± 0.011	-
	1973	994	0.919	0.073 ± 0.008	0.008
	1976	5324	0.931	0.061 ± 0.003	0.008
Apulia: Castellaneta	1971	426	0.906	0.083 ± 0.013	0.011
	1972	1088	0.936	0.055 ± 0.007	0.009
	1973	1030	0.939	0.050 ± 0.007	0.011
	1974	1038	0.928	0.058 ± 0.007	0.014
Otranto	1971	592	0.932	0.054 ± 0.009	0.013
	1972	1062	0.926	0.068 ± 0.008	0.006
	1973	1154	0.950	0.043 ± 0.006	0.007
	1974	1002	0.924	0.068 ± 0.008	0.008
Corato	1971	466	0.944	0.052 ± 0.010	0.004
	1972	314	0.939	0.052 ± 0.012	0.009
	1973	1030	0.947	0.048 ± 0.007	0.005
	1974	1006	0.946	0.046 ± 0.007	0.008
	1978	303	0.940	0.060 ± 0.014	-
Nardò	1978	214	0.930	0.070 ± 0.017	-
Sicily: Archi	1971	400	0.992	0.008 ± 0.004	-
	1972	996	0.948	0.044 ± 0.006	0.008
	1973	1020	0.950	0.048 ± 0.007	0.002
	1974	2030	0.946	0.046 ± 0.005	0.008
Ranna	1971	412	0.947	0.041 ± 0.010	0.012
	1972	868	0.932	0.056 ± 0.008	0.012
	1973	1000	0.952	0.038 ± 0.006	0.010
	1974	1640	0.941	0.051 ± 0.005	0.008
Salemi	1973	954	0.926	0.067 ± 0.008	0.007
Pedalino	1971	324	0.941	0.059 ± 0.013	-
Vittoria	1971	92	0.793	0.207 ± 0.042	-
	1972	764	0.953	0.039 ± 0.007	0.008
	1973	1018	0.928	0.061 ± 0.007	0.011
	1974	1180	0.941	0.048 ± 0.006	0.011

* All the populations were in Hardy-Weinberg equilibrium. ** Part of the present data have already been published elsewhere.
*** SE up to 30% of reported values.

phoretic alleles have been considered. The samples were from natural populations of *Drosophila melanogaster* collected in September and October in various localities of Italy in different years (table). The table shows that the configuration of allelic frequencies at the *Pgm* locus is strikingly similar from locality to locality and in various years. In particular, a) all the populations examined are polymorphic for the $Pgm^{1.00}$ and $Pgm^{0.70}$ electrophoretic alleles, and b) the $Pgm^{1.00}$ allele is the most commonly found throughout the populations and in different years. Similar observations have been made by other authors in many species for various systems[9-15]. However, strikingly similar results are often interpreted from an evolutionary genetics viewpoint in a completely different way. Some authors have as a matter of fact interpreted their data as proof of the action of natural selection[9-11], others, considering the different alleles to be neutral, have argued that these polymorphisms are mainly the consequence of a process of random sampling of the alleles, if there is a certain degree of migration between neighbouring populations[12-15]. However, since in *Drosophila willistoni*[16] and *Drosophila subobscura*[12-15], chromosomal polymorphisms, unlike enzyme polymorphisms, are very different from one locality to the next, different local populations should not represent samples from 1 single panmictic population. Also populations of *Drosophila melanogaster* from different localities can be considered to be different populations, but in this case because of the differences in frequency of *SD* (segregation distorter) chromosomes, 2nd chromosomes sensitive to *SD* and 3rd chromosomes carrying modifiers of the *SD* phenomenon[18,19]. It remains to be seen whether random genetic drift alone can explain the similarity of patterns observed. That is, it is necessary to estimate the size of a population (N_e) during the bottle-neck period. This must be large enough to cover the differences in gene frequencies found from one year to the next. In this case it must be recognized that all these populations derive from a single native population, or at least that they all started out with the same gene frequency. In our calculations we have neglected the mutation rate which for electrophoretically detectable alleles has been estimated as 10^{-8} per locus per generation[14]. We have calculated the probable value of the effective breeding size N_e during the bottle-neck period in the populations examined[20]. The best estimate of N_e is about 5000. If this value is confirmed by field studies (an excellent estimation technique of the population size seems to be that of the mark-release-recapture analysis[21]), then it could be concluded with relative confidence that the PGM electrophoretic polymorphism is maintained in the natural populations studied by random genetic drift. Otherwise we could conclude that besides random genetic drift some form of selection (or co-selection due to linkage disequilibrium effect) is operating on this system.

It is worth emphasizing that a stabilizing selection would make the formal N_e appear larger than the 'true' one by buffering genetic drift. Disruptive selection would lead to an underestimation of N_e. Studies using different markers would make it possible to compare the various N_e values and evaluate the importance of genetic drift and natural selection in maintaining protein polymorphisms in natural populations.

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The effect of lactamide on *Drosophila*

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Summary. Lactamide fed to 3rd instar *Drosophila* larvae induces increased eye facet number in genetically *Bar* individuals and may also produce swollen, shortened legs and notched wings in *Bar* as well as non-*Bar* flies.

The effect of lactamide and related substances on eye facet number in various mutants has been studied extensively[2-4] with particular attention given to the increase in eye facet number caused by feeding lactamide to 3rd instar larvae of the *Bar* genotype; there are no reports, however, of lactamide effects on other organs. Since cells of larval eye imaginal discs are believed to be indistinguishable from cells of other discs both ultrastructurally[5] and biochemically[6] we wished to determine whether lactamide was acting in an organ-specific manner. In this report we show that lactamide can induce wing and leg abnormalities in addition to increasing eye facet number in the *Bar* mutant. In