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Genetica. — *Zygotic and fertility selection for phosphoglucomutase variants in natural populations of* Maniola jurtina *L.* (*Lepidoptera Satyridae*) (*). Nota (**) di VALERIO SCALI e MASSIMO MASETTI, presentata dal Socio M. BENAZZI.

RIASSUNTO. — È stato analizzato il polimorfismo per la PGM, in larve e in adulti da esse derivati, di due popolazioni naturali (S. Marcello e Il Boschetto, Italia centrale) della farfalla satiride *M. jurtina.* Nel passaggio dagli stadi larvali 4° e 5° all'adulto le due popolazioni hanno mostrato cambiamenti simili nelle frequenze dei genotipi e degli alleli: in ambedue le colonie, infatti, rispetto al genotipo Pgm^D/Pgm^D preso come standard, gli individui portatori di Pgm^B sono risultati gravemente svantaggiati; anche gli omozigoti Pgm^C/Pgm^C sono apparsi in svantaggio, specialmente nella popolazione di S. Marcello; gli eterozigoti Pgm^C/Pgm^D hanno invece mostrato una fitness maggiore sia a S. Marcello che a Il Boschetto. Una forte selezione zigotica è risultata perciò operante nelle due popolazioni, soprattutto durante lo stadio di pupa. L'analisi dell'« effetto fertilità » nel confronto fra adulti della generazione parentale e le stesse larve di 4° e 5° stadio da essi derivate, ha mostrato un quadro selettivo opposto: mentre gli eterozigoti Pgm^C/Pgm^D sono svantaggiati, tutte le altre combinazioni alleliche mostrano una fitness superiore a 1. L'insieme dei dati suggerisce fortemente che i vari feno-genotipi PGM hanno un preciso valore adattativo e non sono quindi selettivamente neutri. Inoltre, benché la selezione zigotica qui evidenziata possa ovviamente agire su altre caratteristiche legate alla PGM, il quadro dei cambiamenti della fitness può suggerire una selezione diretta dei vari fenotipi PGM. L'analisi del polimorfismo PGM di *M. jurtina* ha infine rivelato un bilanciamento di svantaggi e vantaggi che genera una selezione endociclica atta a mantenere il polimorfismo stesso ed ha indicato in maniera assai chiara come sia indispensabile analizzare separatamente i vari componenti della selezione al fine di avere un quadro realistico dei trend selettivi, che possono essere diversi o addirittura opposti nei vari momenti del ciclo vitale.

INTRODUCTION

Natural selection has been envisaged as the chief agent of evolution and its evaluation has therefore received careful consideration. Prout [19, 20, 21, 22] has repeatedly pointed out the inadequacy of those analyses which only evaluate the total selection by comparing corresponding stages of successive generations. Actually, four major selection components have been recognised (zygotic, gametic, sexual and fecundity selection) and as a result of the selection component analysis, accurate estimates of selective forces at work during the various stages of the life history have been obtained; the kind and magnitude of selective forces have in turn indicated how polymor-

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phisms can be maintained in experimental and natural populations [4, 5, 6, 7]. We give here the results obtained with a selection analysis conducted on the PGM polymorphism of *Maniola jurtina*.

M. jurtina is a palearctic satyrine butterfly with one generation per year. It goes through five larval instars and the pupal stage before reaching the imaginal condition. Females have only one successful mating occurring at the time of their hatching, which in Italy begins in the second half of May in dry and hot places and in the second half of July in mountain districts. Egg laying occurs either shortly after mating as happens in mountain colonies or after a long imaginal diapause, in coincidence with the hottest season, as has been ascertained in planes and on islands. Caterpillars feed on various grasses, mainly *Poa* and *Agrostis*; they are active during the first instar but soon become torpid, go deep into the turf of their food plants and develop very slowly during winter and early spring, which they usually pass as second and third instars. Moulting to fourth instar often coincides with the resumption of activity during April [23, 24, 25, 15, 26].

In both insular and continental populations, starch gel electrophoresis has revealed the same pattern of 6 PGM allozymes (Pgm^A to Pgm^F), each controlled by a codominant allele of the same gene [16, 17, 3]. Mendelian transmission and segregation of the allozymes were apparent in 2nd instar larvae obtained from single females of known genotype; these findings also showed that larval and adult PGM allozymes are the same and that no developmental changes occur [17].

These results allowed us to analyse whether genotype differences in natural populations exist between larval and adult stages.

MATERIAL AND METHODS

Attempts at capturing with various methods hibernating 2nd and 3rd instar larvae give very poor results. When active 4th and 5th instar caterpillars climb the grass blades at night, they can be collected with a certain success by sweeping grassy areas with a very resistant net. The diagnosis of the caterpillars is quite safe and no mistaken butterfly hatched from controls. Imagines were caught in flight during late morning and early afternoon by the traditional net method. We collected at Il Boschetto (Pisa), a site at sea level where the females experience a summer diapause, and at S. Marcello (Pistoia), 700 meters a.s.l., where no aestivation occurs [23, 24, 15].

The starch gel electrophoresis of PGM allozymes was perfomed for both larvae and adults as previously described [17], the only difference being that for larvae the whole body except the intestine was used for the homogenate. In Hardy-Weinberg tests and in the other comparisons χ^2s with 3 degrees of freedom have been obtained since only the genotype combinations of the 3 commonest alleles (Pgm^B, Pgm^C and Pgm^D) have been treated separately, while all the possible others have been pooled.

RESULTS AND DISCUSSION

Table I reports the larval and adult pheno-genotype distributions, and the fitness of larvae relative to adults in the two colonies, for the 1976 generation. Pgm^D, Pgm^C and Pgm^B are the three commonest alleles in order of decreasing frequency in all samples, while Pgm^F has not been found at Il Boschetto (Table II).

Genotype frequencies appear to be at the Hardy-Weinberg equilibrium, but adults are much closer to it ($\chi^2_{(3)} = 1.18$ with $0.8 > P > 0.7$ for S. Marcello, and $\chi^2_{(3)} = 0.8$ with $0.9 > P > 0.8$ for Il Boschetto) than larvae ($\chi^2_{(3)} = 6.92$ with $0.1 > P > 0.05$ for S. Marcello, and $\chi^2_{(3)} = 3.34$ with $0.5 > P > 0.3$ for Il Boschetto).

The pheno-genotype distributions of larvae are obviously related to those of adults, but sharp differences exist between them. It can be easily seen that, while Pgm^D-bearing individuals increase very much especially in the Pgm^C/Pgm^D combination, Pgm^B-bearing specimens are on the whole reduced in adults, especially in the Pgm^B/Pgm^C and Pgm^B/Pgm^B genotypes; the Pgm^C/Pgm^C homozygotes also decrease from larvae to adults (Table I).

These changes bring about a strong heterogeneity between larval and adult pheno-genotype distribution in the two colonies, giving a $\chi^2_{(3)} = 27.26$ for S. Marcello, and a $\chi^2_{(3)} = 25.05$ for Il Boschetto ($P \ll 0.001$). If we now examine larval to adult viabilities using Pgm^D/Pgm^D as the standard, we can see that, while Pgm^C/Pgm^D shows a slight to strong advantage, all other combinations show reduced fitness, particularly the Pgm^B/Pgm^C and Pgm^C/Pgm^C pheno-genotypes at S. Marcello and the whole set of Pgm^B combinations at Il Boschetto. The only difference worth noting between the two colonies is that Pgm^C combinations are less disadvantaged at Il Boschetto than at S. Marcello.

1976 larval samples also allow us the evaluation of the fertility effect, since for the same two colonies we have data on the adults of the parental (1975) generation [17]. Table III reports the pertinent data to evaluate the viability of expected to observed pheno-genotypes relative to the Pgm^D/Pgm^D standard. Even allowing for some small figures, the general picture is quite clear: the Pgm^C/Pgm^D heterozygote only has a reduced viability while all other combinations show increased fitness; the disadvantage of the Pgm^C/Pgm^D heterozygotes and the advantage of the Pgm^B-bearing specimens are particularly relevant since they completely reverse the zygotic selection trend.

Our analysis has thus revealed that in natural populations of *M. jurtina*, zygotic selection between the final larval instars and the adults is very strong, some pheno-genotypes being almost lethal; we can therefore conclude that the pupal stage must be very critical for selection. We can obviously believe that zygotic selection is acting on other characteristics linked to PGM alleles, rather than directly onto PGM variants. However, the observed changes in the fitness values of the various allele combinations could indicate a direct

TABLE I.

PGM *pheno-genotype distributions in two field populations of* Maniola jurtina *1976 and fitness of larvae to adults relative to* Pgm^D/Pgm^D *as standard.*

S. MARCELLO	AB	AC	BC	BD	CC	CD	CE	DD	DE	DF	Total
Larvae	1	1	14	4	9	14	0	16	3	0	62
Adults	1	1	2	9	14	46	1	49	2	1	126
Fitness	0.326	0.326	0.047	0.735	0.508	1.073	—	1.000	0.218	—	—

IL BOSCHETTO	AD	BB	BC	BD	CC	CD	DD	EE	Total
Larvae	0	3	4	4	6	8	12	1	38
Adults	1	0	5	12	27	78	60	0	183
Fitness	—	—	0.250	0.600	0.900	1.950	1.000	—	—

TABLE II.

Larval and adult PGM *gene frequencies in two field populations of* M. jurtina *1976.*

S. MARCELLO	Pgm^A	Pgm^B	Pgm^C	Pgm^D	Pgm^E	Pgm^F
Larvae 1976	1.62±1.13	15.32±3.23	37.90±4.36	42.74±4.44	2.42±1.38	—
Adults 1976	0.79±0.56	4.76±1.34	30.95±2.91	61.91±3.06	1.19±0.68	0.40±0.40
IL BOSCHETTO	Pgm^A	Pgm^B	Pgm^C	Pgm^D	Pgm^E	Pgm^F
Larvae 1976	—	18.42±4.45	31.58±5.33	47.37±5.73	2.63±1.83	—
Adults 1976	0.27±0.27	4.65±1.10	37.43±2.53	57.65±2.58	—	—

TABLE III.

PGM *pheno-genotype distributions of adult 1975 and larval 1976 field populations of* M. jurtina. *Expected larval frequencies and fitness of adult to larvae, relative to* Pgm^D/Pgm^D *as standard, are given.*

S. MARCELLO	AB	AC	AD	AE	BC	BD	CC	CD	DD	DE	Total
Adults 1975	0	0	2	1	5	7	26	89	57	1	188
Obs. larvae 1976	1	1	0	0	14	4	9	14	16	3	62
Exp. larvae 1976	0.032	0.384	—	—	1.537	2.242	9.348	27.276	19.896	0.384	—
Fitness	(38.859)	(3.238)	—	—	11.327	2.219	1.197	0.638	1.000	9.975	—

IL BOSCHETTO	AB	AC	AD	BB	BC	BD	CC	CD	CE	CF	DD	DE	DF	EE	Total
Adults 1975	1	1	10	1	12	22	42	197	1	1	135	6	1	1	431
Obs. larvae 1976	0	0	0	3	4	4	6	8	0	0	12	0	0	1	38
Exp. larvae 1976	—	—	—	0.070	1.120	1.915	4.481	15.319	—	—	13.094	—	—	0.004	—
Fitness	—	—	—	46.764	3.897	2.279	1.461	0.570	—	—	1.000	—	—	(272.792)	—

selection of PGM variants, since it seems difficult to imagine that adaptively different characters are specifically linked to the various PGM alleles. The kind of results obtained from fertility analysis, although referring to more selection components and therefore of spurious meaning, nonetheless gives an explanation of the mechanism maintaining the PGM polymorphism: at different stages of the life history the same pheno-genotypes enjoy advantages or suffer disadvantages so that carefully balanced frequency adjustments ensue. Owing to this mechanism of endocyclic selection, adults of successive generations may have rather similar genotype frequencies, completely blurring the fact that during the intervening stages strong selective forces are at work. Even if successive generations significantly differ in genotype frequencies (as is here the case, at 5 % and 2 % levels for S. Marcello and Il Boschetto, respectively), total selection figures would be very inaccurate and at any rate they would not tell us anything about the real working of selection. The present analysis has also confirmed that the χ^2 tests for the Hardy-Weinberg equilibrium lack statistical power in assessing significant departures from the expected frequencies. Fitness values, although one must interpret them with caution owing to small figures, seem to suggest that in this polymorphism most genotypes, and therefore alleles, are not adaptively neutral; in addition they may show different adaptive values in the two colonies as is the case of Pgm^C allele. If confirmed by future investigations these results will be at variance with the neutralist hypothesis of protein variation and of course will confirm the selectionist views [11, 10. 13, 14, 12, 1, 2, 9, 27, 18, 8]. These findings also indicate how quick and wide the answer to changing demands at population level can be, when a high degree of genetic diversity is already present as a balanced polymorphism, and that the PGM alleles seem to be of a fast evolving kind.

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