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A Multivariate Analysis of Dominance in *Drosophila*

DOMENICO L. PALENZONA and **GABRIELLA ROCCHETTA**

Institute of Genetics, University of Bologna (Italy)

Summary. Eleven wing measurements in two *Drosophila melanogaster* lines (Canton and FLL) and their reciprocal crosses were analyzed by a multivariate technique in order to investigate changes in variability when dominance is manifested. FLL line was obtained by artificial selection for short wing applied on one measurement on the right wing. Differences between left and right wing were observed in variabilities after selection. The comparison between F_1 and parental populations shows that there is strong evidence for non-additivity which is manifested by a component of the variability due to multiple regression. This is interpreted as meaning that relationships between characters are affected in the heterozygote in a non-additive way, apparently due to interactions among the developmental patterns of the characters considered. It is suggested that a "character" should be defined in such a way as to include its developmental patterns, in order to achieve a better understanding of the dominance phenomenon.

Introduction

A number of experiments indicate that dominance is a character rather than a single gene property. Changes of dominance have been shown to take place in polymorphic populations due to the evolution of a gene complex (Clarke and Sheppard, 1960; Ford, 1955; Sheppard, 1961). Modifier genes affecting the degree of dominance occur widely in many organisms: Ford (1940) and Fisher and Holt (1944) were able to demonstrate changes of dominance under artificial selection, probably selecting for modifiers.

Dominance for quantitative characters is assumed to be a complex phenomenon due to the multiplicity of factors involved. As pointed out by Powers (1944) and Mather (1946), both intra and inter-allelic interactions may be involved if the observed "dominance" is contributed to by all the genes determining a given character. In such a case it becomes difficult to understand the genetic basis of dominance only looking at a one-character model. Moreover, the phenotypic manifestation of interactions between alleles and between genes depends also upon the selective history of the population considered (Mather and Harrison, 1949; Spickett and Thoday, 1966; Palenzona and Alicchio, 1973). This makes the study of selected lines a requirement for understanding the nature of dominance.

An approach to the dominance problem based on a multivariate analysis of selected and unselected populations and their F_1 progenies seems justified therefore.

Material and Methods

Flies from a Canton strain (*Drosophila melanogaster*) were crossed with flies of a population (FLL) derived from the same Canton strain by an artificial selection for short wing. The selection was performed on the 4th longitudinal vein of the right wing on both sexes. On the two parental populations and F_1 reciprocal crosses, eleven distinct measurements were taken with a micrometer on both left and right wings. The data collected are reported in micrometric units (1 unit = 0.025 mm.). The measurements were numbered from 1 to 11 and correspond to the distances between the points indicated in Fig. 1, as follows:

1 = A–C
2 = A–E (selected trait)
3 = F–D
4 = G–I
5 = G–L
6 = C–L
7 = C–E
8 = C–I
9 = L–E
10 = L–I
11 = I–E

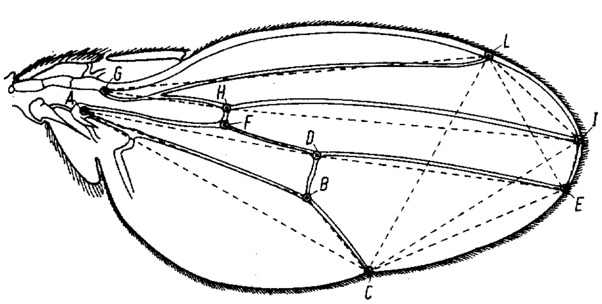

Fig. 1. Scheme of the points on the wing used to take the eleven measurements

Eleven equations of multiple regression were constructed repeatedly taking one measurement as a dependent variable and the remaining ten as the independent ones. Thus for any of the measurements considered it has been possible to partition the Sum of Squares attributable to multiple regression ($S\hat{y}^2$) into two components:

$$S\hat{y}^2 = S\hat{y}^2_{bi} + S\hat{y}^2_{bo}$$

where $S\hat{y}^2_{bi}$ indicates the summed contributions of each independent variable after the remaining ones, and $S\hat{y}^2_{bo}$ is an estimate of interactions between the variables of the set considered, attributable to influences of factors outside the set itself.

Results

Artificial selection applied on the Canton strain has resulted not only in a change in the mean values of the character selected (no. 2) but also in a very similar amount of change in the mean values of all the traits considered. The mean values of reciprocal F_1 crosses between selected (FLL) and unselected (Canton) lines show that there is an almost complete dominance of Canton over FLL for all the characters considered.

There seems to be no appreciable difference between data collected on the right wing and that observed on the left one (tables 1 and 2). Estimates of variability, reported in Tables 3 and 4 as mean sum of squares, indicate that there are differences in the effect of selection both among characters and between right and left wings. Differences are also detectable between reciprocal crosses. In F_1 populations there is a general tendency for the variance values to approximate towards the smallest of the parents. Comparing the Canton and FLL populations, it may be noticed that variance estimates of the right wing measurements are changed following artificial selection: in particular variance is reduced for trait 2 (the selected character) as well as for traits 1, 6, 7, 8, which all belong to the lower portion of the wing except for number 6, which is partly in the lower and partly in the upper portion. For the other traits considered, variance estimates are unaffected or increased after selection. The measurements taken on the left wing show an increase after selection for all the traits except 1, 6, 10, 11, which seem to be unaffected.

Table 1. *Mean values ($\bar{x}$) ± standard errors (s.e.) of the eleven traits in the populations studied. Right wing*

Traits	Canton	FLL	Canton × FLL	FLL × Canton
	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.
1	45.2 ± .10	37.4 ± .13	44.9 ± .07	45.6 ± .10
2	68.8 ± .16	53.1 ± .19	67.1 ± .12	68.0 ± .13
3	15.2 ± .06	11.1 ± .09	14.7 ± .07	14.6 ± .06
4	69.2 ± .12	52.9 ± .25	67.4 ± .12	67.9 ± .13
5	55.9 ± .15	43.5 ± .25	54.9 ± .14	55.5 ± .13
6	54.5 ± .12	43.8 ± .13	52.7 ± .10	52.9 ± .09
7	47.7 ± .13	34.5 ± .13	45.1 ± .11	45.0 ± .10
8	56.2 ± .13	41.7 ± .13	53.3 ± .12	53.4 ± .10
9	33.4 ± .08	26.2 ± .11	32.3 ± .11	32.1 ± .07
10	28.5 ± .08	21.5 ± .13	27.3 ± .09	27.3 ± .09
11	11.0 ± .03	9.0 ± .06	10.8 ± .06	10.7 ± .06

Table 2. *Mean values ($\bar{x}$) ± standard errors (s.e.) of the eleven traits in the populations studied. Left wing*

Traits	Canton	FLL	Canton × FLL	FLL × Canton
	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.	$\bar{x}$ ± s.e.
1	45.2 ± .09	37.8 ± .14	45.1 ± .09	46.1 ± .10
2	68.8 ± .12	53.5 ± .26	67.3 ± .13	68.5 ± .14
3	15.1 ± .05	11.2 ± .12	14.8 ± 0.7	14.7 ± .06
4	69.3 ± .13	52.8 ± .28	67.6 ± .13	67.9 ± .14
5	55.6 ± .12	43.1 ± .27	55.1 ± .15	55.3 ± .14
6	54.5 ± .09	44.1 ± .16	52.9 ± .10	52.9 ± .10
7	47.5 ± .09	34.7 ± .19	45.3 ± .10	45.1 ± .11
8	56.1 ± .09	42.0 ± .20	53.6 ± .10	53.5 ± .12
9	33.6 ± .07	26.4 ± .13	32.1 ± .09	31.9 ± .08
10	28.7 ± 0.8	21.6 ± .13	27.2 ± .08	27.0 ± .09
11	11.0 ± .03	9.0 ± .05	10.7 ± .06	10.7 ± 0.5

Table 3. *Variance estimates for the eleven traits in all the populations studied. Right wing*

Traits	Canton	FLL	Canton × FLL	FLL × Canton
1	0.9295	0.6444	0.3789	0.7247
2	2.2277	1.2786	1.0452	1.2571
3	0.2732	0.2944	0.3031	0.2354
4	1.3126	2.3302	0.9697	1.1521
5	2.1146	2.3135	1.3201	1.2821
6	1.2520	0.6183	0.6957	0.5928
7	1.4037	0.5992	0.7805	0.7268
8	1.5508	0.6183	0.9263	0.7171
9	0.5283	0.4064	0.8061	0.3759
10	0.5930	0.6000	0.5145	0.5767
11	0.0794	0.1143	0.2766	0.2113

Table 4. *Variance estimates for the eleven traits in all the populations studied. Left wing*

Traits	Canton	FLL	Canton × FLL	FLL × Canton
1	0.7245	0.7447	0.5511	0.7340
2	1.3641	2.5886	1.0780	1.3832
3	0.2145	0.5225	0.3355	0.2576
4	1.4453	2.8063	1.1795	1.4246
5	1.2911	2.7868	1.5260	1.3832
6	0.7436	0.8859	0.6334	0.7503
7	0.7058	1.3814	0.6321	0.8963
8	0.7097	1.4159	0.7417	1.0644
9	0.3853	0.5811	0.5452	0.4151
10	0.5046	0.5751	0.4693	0.6079
11	0.0677	0.0826	0.2251	0.1938

The differences observed between the right and left wings in parental populations are strongly reduced in the F_1 progenies.

In Tables 5, 6, 7, 8, the estimates are shown of the mean sum of squares attributable to multiple regression ($V\hat{y}^2$) and of the ratios $V\hat{y}^2_{bi}/V\hat{y}^2$ and $V\hat{y}^2_{bo}/V\hat{y}^2$, that is, the ratios between the variances of the single components and the mean sum of squares attributable to regression. It may be observed that values of $V\hat{y}^2$ are changed after artificial selection mainly on the right wing (on which selection has been performed); moreover, the change is larger for the traits 1, 2, 6, 7, 8, which belong to the lower portion of the wing, than for the others. Estimates of $V\hat{y}^2$ show behaviour very similar to that of the variances reported in tables 3 and 4.

Considering the values of the components $V\hat{y}^2_{bi}$ and $V\hat{y}^2_{bo}$ relative to $V\hat{y}^2$, it may be noticed that they seem

Table 5. *Values of $V\hat{y}^2$, $V\hat{y}^2_{bi}/V\hat{y}^2$, $V\hat{y}^2_{bo}/V\hat{y}^2$; parental populations. Right wing*

	Traits	$V\hat{y}^2$	$V\hat{y}^2_{bi}/V\hat{y}^2$	$V\hat{y}^2_{bo}/V\hat{y}^2$
Canton	1	5.816	0.039	3.767
	2	16.874	0.036	4.279
	3	0.720	0.058	0.637
	4	7.210	0.041	3.364
	5	14.538	0.039	3.746
	6	9.074	0.037	4.091
	7	10.674	0.039	3.771
	8	12.100	0.038	3.865
	9	3.294	0.052	1.661
	10	3.549	0.055	1.166
	11	0.078	0.056	1.099
FLL	1	1.662	0.052	1.647
	2	3.683	0.045	2.711
	3	0.278	0.051	0.570
	4	7.348	0.054	1.371
	5	7.182	0.058	0.694
	6	1.632	0.048	2.292
	7	1.795	0.053	1.457
	8	1.793	0.049	2.136
	9	1.044	0.050	2.027
	10	1.406	0.046	2.597
	11	0.290	0.055	1.169

Table 6. *Values of $V\hat{y}^2$, $V\hat{y}^2_{bi}/V\hat{y}^2$, $V\hat{y}^2_{bo}/V\hat{y}^2$; parental populations. Left wing*

	Traits	$V\hat{y}^2$	$V\hat{y}^2_{bi}/V\hat{y}^2$	$V\hat{y}^2_{bo}/V\hat{y}^2$
Canton	1	4.027	0.044	2.961
	2	10.143	0.042	3.328
	3	0.511	0.047	2.589
	4	11.054	0.040	3.515
	5	8.962	0.044	3.000
	6	4.491	0.039	3.686
	7	4.323	0.044	2.891
	8	4.689	0.041	3.381
	9	1.886	0.055	1.159
	10	2.545	0.056	1.029
	11	0.157	0.060	0.401
FLL	1	2.271	0.042	3.226
	2	8.806	0.038	3.964
	3	1.007	0.043	3.106
	4	9.547	0.036	4.245
	5	8.298	0.038	3.839
	6	2.383	0.044	2.876
	7	4.406	0.040	3.637
	8	4.673	0.039	3.723
	9	1.615	0.057	0.806
	10	1.520	0.057	0.907
	11	0.197	0.058	0.772

Table 7. *Values of $V\hat{y}^2$, $V\hat{y}^2_{bi}/V\hat{y}^2$, $V\hat{y}^2_{bo}/V\hat{y}^2$; F_1 populations. Right wing*

	Traits	$V\hat{y}^2$	$V\hat{y}^2_{bi}/V\hat{y}^2$	$V\hat{y}^2_{bo}/V\hat{y}^2$
Canton × FLL	1	1.607	0.687	3.134
	2	6.340	0.640	3.595
	3	0.578	0.698	3.016
	4	5.808	0.637	3.629
	5	7.419	0.669	3.308
	6	3.601	0.662	3.373
	7	4.073	0.675	3.228
	8	5.280	0.626	3.376
	9	4.063	0.961	0.392
	10	2.627	0.971	0.291
	11	0.565	0.996	0.036
FLL × Canton	1	3.866	0.762	2.376
	2	6.948	0.726	2.739
	3	0.313	0.910	0.895
	4	5.920	0.688	3.123
	5	4.403	0.729	2.706
	6	2.187	0.732	2.672
	7	1.862	0.767	2.329
	8	3.137	0.710	2.985
	9	1.568	0.804	1.957
	10	2.334	0.862	1.376
	11	0.343	0.871	1.284

Table 8. *Values of $V\hat{y}^2$, $V\hat{y}^2_{bi}/V\hat{y}^2$, $V\hat{y}^2_{bo}/V\hat{y}^2$; F_1 populations. Left wing*

	Traits	$V\hat{y}^2$	$V\hat{y}^2_{bi}/V\hat{y}^2$	$V\hat{y}^2_{bo}/V\hat{y}^2$
Canton × FLL	1	2.402	0.623	3.765
	2	5.990	0.573	4.266
	3	0.906	0.662	3.376
	4	7.102	0.585	4.145
	5	8.774	0.636	3.640
	6	3.397	0.605	3.951
	7	3.358	0.648	3.517
	8	4.226	0.610	3.902
	9	3.103	0.965	0.348
	10	2.555	0.977	0.229
	11	0.605	0.996	0.037
FLL × Canton	1	4.354	0.724	2.761
	2	8.625	0.668	3.322
	3	0.667	0.679	3.208
	4	8.647	0.591	4.088
	5	7.448	0.672	3.279
	6	3.631	0.683	3.167
	7	4.993	0.682	3.176
	8	6.373	0.667	3.330
	9	1.890	0.915	0.850
	10	2.780	0.899	1.009
	11	0.325	0.942	0.583

quite constant within each population considered: this suggests that there is a constant proportionality between the components and their total, irrespective of the independent variable considered. The relative value of $V\hat{y}^2_{bi}$ over $V\hat{y}^2$ seems to be only slightly increased after selection in data from the right wing, while it is seemingly unaffected in data from the left one. The same estimate is, however, strongly increased in data from the F_1 population, while the relative value of $V\hat{y}^2_{bo}$ over $V\hat{y}^2$ in the F_1 generation maintains about the same values observed in the parental populations.

The amount of change observed in the F_1 in relation to the differences existing between the parental populations indicates an interaction in the genetic control of correlations between traits.

Discussion

Dominance is usually defined by comparison between the average phenotypes of parental and F_1

populations; such a comparison requires, as a criterion of comparability, that random effects, which affect the mean values, be the same in the populations compared. If this requirement is not fulfilled, the comparison between average values is meaningless.

When dominance is present, two conditions must be assumed: namely, equality of variances and additivity of gene expression, in order to make the F_1 and parental populations comparable. These assumptions are rarely met, thus restricting the field of comparability between F_1 and parental populations. A solution to this problem has been proposed involving an appropriate change of scale resulting in additive gene expression: this solution however implies a loss of information due to the *a posteriori* choice of the scale.

Another solution, which we are concerned with in the present paper, consists of a redefinition of the dominance concept so as to include a variability estimate in addition to the mean value. In fact the estimates of variability are always comparable provided the characters considered have similar frequency distributions.

In order to understand the nature of a character's variability as well as its genetic basis, the effects of its genetic background must be taken into account. For this reason, in the present paper each of eleven traits, all being measurements of *Drosophila* wing, was defined in terms of mean values and phenotypic variance. In the phenotypic variance a portion was distinguished, attributable to multiple regression of each trait on the other ten considered; the latter variance estimate was then partitioned into variance due to regression on the single independent variables ($S\hat{y}^2_{bi}$), and into a portion due to residual interaction among the same variables because of the effects of agents not considered in the regression equation ($S\hat{y}^2_{bo}$). Since the eleven characters belong to the same developmental unit, a certain amount of relationship is expected between variance and covariance values. This is indeed the case as shown by the results obtained: there is an obvious parallelism in the variations of variance and covariance in the traits considered. This indicates that, in general, the variability of one trait cannot be separated from that of the remaining phenotype.

The results obtained analyzing the variances of the two populations (Canton and FLL) show that following the artificial selection performed, differences are manifested between the right and left wings and between the upper and lower portions of the right wing (where selection was applied); these differences seem to be attributable to variations in the wing developmental pattern. Although the absolute values of phenotypic variances and variances due to multiple regression are affected in different ways in the various traits considered, the relative values of their components are changed by a fairly constant proportion of the total variability: this is shown by the remarkably constant values of the ratios between components and total variance within each population.

Comparing now the F_1 population with its parents, it may be observed that the variability in the former, shows values approximating to the lowest of the two parents, irrespective of the dominance exhibited by the mean value. In fact, F_1's mean values are always nearly identical to Canton's.

Taken with the variability results, this suggests that the similarity of dominance, as shown by mean values of the eleven characters, has been achieved through different patterns. There should be, therefore, some sort of control over the mean phenotypic manifestations of the characters considered. When the ratios between the component $S\hat{y}^2_{bi}$ and the total variance attributable to multiple regression are considered, it may be noticed that there is a striking increase in the F_1 compared with the parental lines; this difference is quite a bit larger than that between the parents, suggesting the existence of some kind of non-additive effect in the reciprocal influences of the traits considered. Since differences between the left and right wings have disappeared in the F_1 generation, it must be concluded that changes in developmental patterns observed following the artificial selection applied are modified in the heterozygote.

Thus a conclusion seems to have been arrived at, that variability, like mean value, may show non-additive changes in the heterozygote which are at least in part traceable to agents controlling the developmental patterns. This conclusion has long been known but the way it has been reached is not, and it may bear some relevance to the understanding of biological interactions in general and of dominance in particular. If developmental changes take place in the F_1 which affect the relationships between traits, it seems no longer meaningful to study interactions on the basis of one character alone.

The rationale of genetics is in fact based on the assumption that direct links do exist between additive genetic effects and the underlying genotype. This can hold true only if the developmental patterns leading to a particular phenotype depend on one, and only one, genotype. Since this seems not to be the case in the results given in the present paper, it must be suggested that either the character should be defined as to account for the developmental patterns by which it is linked to its genotype, or it would be meaningless to try to uncover its genetic basis and to distinguish between additive and interaction effects in the phenotype.

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Professor D. L. Palenzona
Institute of Genetics
University of Bologna
Via F. Selmi 3
40126 Bologna (Italy)