STUDIES ON NATURAL POPULATIONS OF DROSOPHILA. IV. GENETIC VARIANCES OF AND CORRELATIONS BETWEEN FOUR CHARACTERS IN D. MELANOGASTER AND D. SIMULANS

A. O. TANTAWY AND F. A. RAKHA

Faculty of Agriculture, University of Alexandria, Alexandria, U.A.R.

R ESEMBLANCE between relatives with respect to a given quantitative character is a basic genetic phenomenon; the degree of resemblance determines the amount of additive genetic variance. The causes for such resemblance are related not only to genetics but also to environment. Therefore, the phenotypic value for a given individual is the sum of genetic and environmental effects (REEVE and ROBERTSON 1953).

Most characters in Drosophila are highly responsive to environmental changes (TANTAWY and MALLAH 1961) and only a proportion of the total phenotypic variance is actually accounted for by gene action. In selection programs (e.g. TANTAWY. MALLAH and TEWFIK 1964) it is essential, in some experiments, to divide the total variation of a given trait into its various components, particularly that component due to the additive gene effects. Correlation coefficients between various characters are needed; the genetic correlation is important because the response to selection for the primary character may influence the secondary characters (REEVE and ROBERTSON 1953; CLAYTON, KNIGHT, MORRIS and ROBERTSON 1957).

The present experiments were undertaken to study the genetical and environmental effects on the total phenotypic value for a given character in populations of two Drosophila species. Heritability estimates were made for each of the characters wing length, thorax length, longevity of adult flies and lifetime egg production. and correlation coefficients were determined between each pair.

TECHNICAL PROCEDURE

The initial foundation population: Populations used in the present experiments are similar to those used by TANTAWY and MALLAH (1961) which were captured at the University of Alexandria Farm. In each species eggs (not more than 70 per vial) from the mass-mating population were cultured in well yeasted food vials in ten replicates. After emergence, virgin females were separated from males. Twenty pairs, ten on each day, from each replicate (given a total of 200 pairs) were measured for wing and thorax length. The measured flies were also used for estimating the lifetime egg production and the longevity of both sexes. Measurements of wing and thorax lengths, lifetime egg production and longevity were carried out as described by TANTAWY (1961a).

Progeny tests: Eggs from both species were cultured as before in 20 food vials. After emer-

gence virgin females were obtained and 20 pairs of flies from each vial, ten on each day, were measured for wing and thorax lengths. Random pair-matings were carried out among the measured flies of each vial; lifetime egg production and longevity were also estimated. Eggs from the 400 pair matings were cultured in food vials, and after emergence of the F_1 progeny, virgin females were also obtained. Five males and five females from the progeny of each pair-mating were used for measuring wing and thorax lengths, as well as lifetime egg production and longevity. Heritability of each character was estimated by doubling the phenotypic correlation between mothers and daughters.

Since the statistical analyses indicate no significant differences between replicates, the results were combined and presented as weighted means.

All the experimental work were carried out under constant temperature of $25 \pm 0.5°C$.

RESULTS

Comparisons between D. melanogaster *and* D. simulans: Table 1 shows the absolute means for the four characters studied. The results indicate clearly that the two species are different; *melanogaster* displays greater measurements for each trait than *simulans*, and *melanogaster* females lay significantly ($P < 0.01$) more eggs. Moreover, eggs of *D. melanogaster* are the more viable (TANTAWY and MALLAH 1961). In both species females have significantly ($P < 0.01$) longer wings than males, and females of both species live longer than males (though not significantly so).

Total phenotypic correlations: Table 2 presents the various correlation coefficients. There are clearly significant positive phenotypic correlations between

TABLE 1

Means (1/100 mm) for wing length, thorax length; longevity (days) and lifetime egg production (average per female) with their respective coefficients of variation (C.V.). n = 200

| Characters | D. melanogaster | | | | D. simulans | | | |
| | Males | | Females | | Males | | Females | |
	Means	C.V.	Means	C.V.	Means	C.V.	Means	C.V.
Wing length (W)	175.32	2.95	204.17	3.20	173.69	3.89	200.83	3.62
Thorax length (T)	89.25	3.95	103.25	3.72	85.85	4.27	100.11	4.49
Longevity (L)	14.06	29.44	14.80	31.01	8.95	34.52	12.59	32.84
Lifetime egg production (G)	. . . .	. . . .	389.50	60.12	. . . .	. . . .	191.75	80.23

TABLE 2

Observed total phenotypic correlations between different characters

Correlations between	D. melanogaster	D. simulans
Wing length—Thorax length	0.5775 ± 0.116	0.5840 ± 0.089
Wing length—Egg production	0.2440 ± 0.137	0.2189 ± 0.118
Wing length—Longevity	0.2197 ± 0.138	0.2143 ± 0.124
Thorax length—Egg production	0.5055 ± 0.112	0.2508 ± 0.117
Thorax length—Longevity	0.3315 ± 0.133	0.1190 ± 0.112
Longevity—Egg production	0.7568 ± 0.137	0.4035 ± 0.110

Degrees of freedom = 380.

the different characters which raises the question as to the origin of such an association and whether it is due to environment, to heredity or to both. SANG (1950) has noted that the smaller flies which result from crowded conditions during growth lay fewer eggs. ROBERTSON (1957b) reported similar positive correlations between body size and egg production in *D. melanogaster*. TANTAWY and VETUKHIV (1960) and TANTAWY (1961b) showed positive correlations among the same four different characters used in the present study, but in *D. pseudoobscura*; a given reduction in size in *D. pseudoobscura* leads to a proportional reduction in egg production and longevity as well.

Heritability estimates: It seems to be very important to give all the observed parent (mothers)-offspring (daughters) correlations for both species (Table 3) which includes not only the correlations with respect to the same characters but also the cross correlations, e.g. parent's wing *vs.* offspring's thorax. The results indicate positive correlations between different characters. The parent offspring correlation ($r_{P_X O_X}$) was used in estimating the heritability ($h^2 = 2\,r_{P_X O_X}$) of each character and $e^2 = 1 - h^2$. The results are presented in Table 4, where h and e have their usual meanings and usefulness. The results indicate clearly that the metric characters wing length and thorax length are more heritable than longev-

TABLE 3

Parent-offspring correlations (e.g., wing vs. *wing) and the cross correlations*
(e.g., wing vs. *thorax)*

Parents	Offspring			
	Wing length	Thorax length	Longevity	Egg production
a. *Drosophila melanogaster*				
Wing length	0.1231 ± 0.032	0.0819 ± 0.021	0.0150 ± 0.025	0.0005 ± 0.039
Thorax length	0.0957 ± 0.025	0.1017 ± 0.020	0.0104 ± 0.037	0.0014 ± 0.048
Longevity	0.0750 ± 0.049	0.0889 ± 0.034	0.0564 ± 0.043	0.0058 ± 0.033
Egg production	0.0019 ± 0.054	0.0014 ± 0.042	0.0004 ± 0.038	0.0128 ± 0.026
b. *Drosophila simulans*				
Wing length	0.1090 ± 0.031	0.1780 ± 0.022	0.0303 ± 0.024	0.0004 ± 0.038
Thorax length	0.0436 ± 0.034	0.1165 ± 0.025	0.0221 ± 0.041	0.0010 ± 0.051
Longevity	0.0708 ± 0.045	0.1228 ± 0.036	0.0730 ± 0.045	0.0030 ± 0.038
Egg production	0.0026 ± 0.049	0.0015 ± 0.039	0.0014 ± 0.039	0.0556 ± 0.037

TABLE 4

Heritability ($h^2 = 2\,r_{P_X O_X}$), $e^2_X = 1 - h^2_X$ *for each character as well as* h *and* e *values.*
Number of matings = 400

Characters	D. melanogaster				D. simulans			
	h^2	e^2	h	e	h^2	e^2	h	e
Wing length	0.2462	0.7538	0.4962	0.8682	0.2180	0.7820	0.4669	0.8843
Thorax length	0.2034	0.7966	0.4510	0.8926	0.2330	0.7670	0.4827	0.8758
Longevity	0.1129	0.8871	0.3360	0.9419	0.1460	0.8540	0.3821	0.9241
Egg production	0.0257	0.9743	0.1603	0.8971	0.1112	0.8888	0.3335	0.9428

ity and egg production (to be referred to as fitness character). The value of h^2 expresses the proportion of the total variance that is attributable to the average effects of genes; this is what determines the degree of resemblance between relatives. The total variation for a given character includes additive, nonadditive and environmental causes; nonadditive causes play a great role in the total variation of the fitness characters than the metric ones. Similar results were reported by ROBERTSON (1957b).

Knowledge of the degree of the correlation between phenotypic and breeding value (i.e., h) for a given character is important in the prediction of the response to selection. The results indicate that the breeding values for metric characters are higher than those of fitness ones, while e values are reversed in favor of the latter. These results agree with those reported by ROBERTSON (1957b) in showing the gradation of the heritability estimates for metric and fitness characters in *D. melanogaster*.

Genetic and environmental correlations: Estimates of the genetic (r_G) and environmental (r_E) components of the phenotypic correlations, e.g. between the two characters X and Y, could be given from the following equations, where P and O denote parents and offspring.

$$r_{G_X G_Y} = 2\sqrt{r_{P_X O_Y}\, r_{P_Y O_X}}/h_X h_Y$$

$$r_{E_X E_Y} = [r_{O_X O_Y} - h_X h_Y r_{G_X G_Y}]/e_X e_Y$$

The quantities $r_{G_X G_Y}\, h_X h_Y$ and $r_{E_X E_Y}\, e_X e_Y$ should add up exactly to r_{XY} of Table 2.

The results for the genetic and environmental correlations between different characters in both species are presented in Table 5. The results for the genetic

TABLE 5

Genetic (r_G) *and environmental* (r_E) *correlations between different characters*

Correlations between*	(1) $2\sqrt{r_{P_X O_Y}\, r_{P_Y O_X}}$	(2) $h_X h_Y$	(1)/(2) $r_{G_X G_Y}$ (r$_G$)	(3) $r_{O_X O_Y}$	(4) (3)—(1)	(5) $e_X e_Y$	(4)/(5) $r_{E_X E_Y}$ (r$_E$)
a. *Drosophila melanogaster*							
Wing—Thorax	0.1771	0.2238	0.7913	0.5775	0.4004	0.7749	0.5167
Wing—Egg	0.0020	0.0795	0.0252	0.2440	0.2420	0.8570	0.2824
Wing—Longevity	0.0671	0.1667	0.4025	0.2197	0.1526	0.8178	0.1866
Thorax—Egg	0.0028	0.0723	0.0387	0.5055	0.5027	0.8810	0.2706
Thorax—Longevity	0.0608	0.1515	0.4013	0.3315	0.2707	0.8406	0.3220
Longevity—Egg	0.0030	0.0539	0.0557	0.7568	0.7538	0.9297	0.8108
b. *Drosophila simulans*							
Wing—Thorax	0.1762	0.2254	0.7817	0.5840	0.4078	0.7745	0.5265
Wing—Egg	0.0020	0.1557	0.0128	0.2189	0.2169	0.8337	0.2602
Wing—Longevity	0.0926	0.1784	0.5191	0.2143	0.1217	0.8172	0.1489
Thorax—Egg	0.0025	0.1610	0.0155	0.2508	0.2483	0.8257	0.3007
Thorax—Longevity	0.1042	0.1844	0.5651	0.1190	0.0148	0.8093	0.0183
Longevity—Egg	0.0041	0.1274	0.0322	0.4035	0.3994	0.8712	0.4584

* Degrees of freedom = 380.

correlation (r_G) between wing-thorax lengths, wing length-longevity and thorax length-longevity are high in both species, indicating that flies with longer wings have greater thorax length and live longer than small flies. These results agree with the findings of TANTAWY and VETUKHIV (1960) in *D. pseudoobscura*. Other genetic correlations, particularly those with egg production, are very low, indicating that a change made by selection for wing length in Drosophila is not accompanied by a similar change in lifetime egg production. REEVE (1954) reported, in spite of the value of 0.27 as the genetic correlation between body size and egg production in *D. melanogaster*, that a change in the former character made by selection did not lead to a parallel change in the latter. ROBERTSON (1957b) stated that in only one comparison after five generations of selection was there clear evidence of correlated change in egg production; in others, the differences in the output between large, small and unselected strains are negligible.

Environmental correlation (r_E) between different traits, which is due to the correlation of environmental deviations together with nonadditive genetic ones, shows how the genetic and environmental causes of correlation combine together to give the total phenotypic correlations. The results (Table 5) indicate that if both characters possess low heritability (e.g., longevity and egg production) then the phenotypic correlation between them is determined chiefly by environmental correlation, and on the other hand if they display high additive genetic variance (e.g., wing and thorax lengths) then the genetic correlation is more important. The results obtained for wing and thorax lengths confirm those given by REEVE and ROBERTSON (1953), who reported genetic and environmental correlations of 0.75 and 0.5, respectively. REEVE and ROBERTSON (1954) stated "the genetic and environmental variations affecting a quantitative character should at least partly mimic each other's effects, since they must often influence the same chemical processes. Thus, both genetic and environmental factors affecting wing and thorax length in Drosophila cause partly correlated and partly uncorrelated variation, so that the genetic and environmental correlations are typically of the same order." The present results agree, in general, with those reported by the previous authors.

Conclusions: For a detailed study of the genetic variance in wild populations of Drosophila, it is essential to investigate and compare the properties of the genetic variation in many different characters. Various authors attacked such a problem in *D. melanogaster*, e.g. ROBERTSON and REEVE (1952); REEVE and ROBERTSON (1953); TANTAWY (1964) and TANTAWY *et al.* (1964) working on body size, CLAYTON *et al.* (1957) on bristle numbers, ROBERTSON (1957a) on ovary size and ROBERTSON (1957b) on egg production. The present investigation adds more information on the inheritance of quantitative characters in both *D. melanogaster* and *D. simulans* and the relationship between some of the different characters, namely wing length, thorax length, longevity and lifetime egg production.

The results as presented in Tables 1 and 4 indicate clearly that the characters with lower heritability estimates show greater phenotypic variation. Similar

results were reported by ROBERTSON (1957b) on *D. melanogaster* and by TANT-
AWY (1961b) on *D. pseudoobscura*. It is interesting, however, that fitness char-
acters having lower heritability estimates experienced a greater reduction during
inbreeding than metric ones (TANTAWY 1959).

The higher heritability estimates for wing and thorax lengths indicate that
selection for longer or shorter dimensions is more effective than that for egg
production or longevity. These results agree with those reported by different
investigators working on such a problem (for review and references see TANT-
AWY *et al.*, 1964). The genetic correlation can be utilized more accurately as a
basis for selection for a given character than the phenotypic one, if both are
estimated with equal accuracy. For instance, selection for wing length would be
accompanied by a similar change in the same direction for thorax length or *vice
versa* (ROBERTSON and REEVE 1952; REEVE 1954; TANTAWY 1959; TANTAWY
et al. 1964), to a lesser degree for longevity, but not for egg production (ROBERT-
SON 1957b). From the various correlation coefficients, one may conclude that egg
production is correlated with body size and with longevity through nonadditive
gene effects; gene-environment interaction may play a great role in such an
association. This is likely to be important in view of the sensitivity of growth to
nutritional variation (ROBERTSON 1963). If most individuals never attain their
maximum potential size, larger individuals will be favoured by virtue of their
greater output and might expect a clear-cut correlation between body size and
egg production, and probably also growth rate.

Few experiments have been performed to check the adequacy of the response
to selection for a primary character on correlated ones. For instance, REEVE
(1954), CLAYTON *et al.* (1957) and ROBERTSON (1957a,b) all reported that the
observed response to selection for a given metric character in *D. melanogaster*
fits well with the theoretical expectation. Therefore, the next paper will deal with
long term two-way selection for wing length and its effects on the other three
correlated characters.

SUMMARY

Correlation coefficients were determined between four different characters,
wing length, thorax length, lifetime egg production and the longevity of adult
flies. The total phenotypic $(r_{o_X o_Y})$ and the cross correlations $(r_{P_X o_Y})$ between
each two characters indicate clear positive values. Wing and thorax lengths dis-
play higher heritability estimates $(h^2 = 2r_{P_X o_X})$ than egg production or longev-
ity, in both species. Genetic correlations involving wing length, thorax length
and longevity are high, while those including egg production are very low; all
the genetic correlations are positive. Environmental correlations between differ-
ent characters were calculated and discussed.

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