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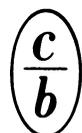
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ANALYSIS OF STRUCTURE OF INTRAPOPULATIONAL VARIATION
IN QUANTITATIVE TRAITS

N. V. Glotov, V. V. Tarakanov, L. A. Gritsenko,
and M. I. Rakhman

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The results are presented of an investigation of the reproducibility in time of the structure of variation in natural populations of *Drosophila* and the plum *Prunus divaricata*. Estimates of the components of intrapopulational variation for a series of quantitative traits were obtained by the analysis of variance (model with random effects). It was shown that in spite of the possible large differences in the average values of traits, the structure of variation is quite stable.

When studying the structure of populational variation in a species throughout or in a portion of the distribution range, it is first necessary to estimate the stability of this structure in time. The investigator is usually unable to obtain information on all populations of interest to him in a short interval of time, and in this case material is gathered over several years. On the other hand, if the material is gathered throughout the distribution range during a short period and only once, which often happens in population work due to its organizational-technical complexity, the question arises as to how precisely such "instantaneous photography" reflects the true populational structure. Such circumstances are, as a rule, understood, and sometimes control observations are made, but these questions are rarely subjected to specific analysis.

We examined the structural stability of the populational variation of quantitative traits in *Drosophila* and the plum *Prunus divaricata* Led. For study of the quantitative traits of *Drosophila* (*D. melanogaster* Mg.) the flies were trapped in orchards of the Ubinskaya Station (Krasnodarskii Territory) in August 1980 (subsequently, sample A-80), in September 1980 (S-80), and in July, August, and September, 1981 (J-81, A-81, and S-81, respectively). At ten sites situated more or less evenly on an area of about 1 × 3 km, 25 females were trapped at each time. The following traits were considered: 1) The distance between ends of the fourth and fifth longitudinal wing veins (subsequently, "wing length"); 2) the length of the femur of the third pair of legs (both traits measured in ocular-micrometer units); 3) number of sternopleural bristles; 4) number of abdominal bristles; 5) number of branches of the arista. Four traits were considered in each individual separately on the left and right sides of the body, while the number of abdominal bristles was considered separately on the fourth and fifth sternites. Thus, we were able to subtract the metameric (bilateral) variation from the total populational variation.

The average values of traits for individual samples could differ statistically significantly. For example, at site 1 the average wing length in the sample S-80 (139.0 ± 1.51) differs at the 5% level from A-80 (134.5 ± 1.60) and J-81 (133.4 ± 1.74) and at the 1% level from A-81 (133.0 ± 1.72) and S-81 (132.7 ± 1.40). In sample A-80 the greatest difference between means was obtained for sites 7 (129.8 ± 2.22) and 8 (143.8 ± 0.93); it is significant at the 1% level, as are another nine differences of the 45 possible. No systematic tendency for change in the means could, however, be demonstrated either in space or in time. Similar results were obtained for the other traits.

The variation in the average values of traits in a single population at different sampling times is well known and is apparently explained mainly by the influence of environmental factors (Tantawy, 1964; Sokoloff, 1965; Bryant, 1977). In our case this may be explained by differences in the weather conditions and conditions of *Drosophila* nutrition. Tarakanov (1982), for example, notes that in 1980 there was a good prune harvest and a poor

A. A. Zhdanov Leningrad State University. Translated from *Ékologiya*, No. 3, pp. 13-18, May-June, 1986. Original article submitted July 16, 1985.

TABLE 1. Contribution of Influence of Factors during Popu-
lational Variation in *Drosophila*, %

Trait	Collection site	Collection time	Site-time interaction	Individual	Residual variation
Wing length	0	5,7	3,4	89,1	1,8
Thigh length	0	4,3	1,9	92,2	1,6
No. of sternopleural bristles	0	0	0	51,0	49,0
No. of abdominal bristles	0	0	0	60,2	39,8
No. of arista hairs	0	1,1	0	33,1	65,8

apple harvest in orchards of the Ubinskaya Station; in 1981, by contrast, there was an abundance of apples and very few prunes.

The structure of variation for each trait was analyzed in three-factor dispersion analysis: Two factors (sampling site and sampling time) are grouped with overlap, while a third — the females at each site (i.e., at a given site at a given time) — hierarchically with respect to the first two. The residual (uncontrolled) variation is estimated by repeated measurements for each individual. We considered all factors as random, i.e., as a random sample of the levels of a factor out of the aggregate of all its possible values. The structure of variation of different traits is shown in Table 1; the estimate of the corresponding variance was calculated only in the case where the influence of the factor was significant at the 5% level; however, $p < 0.01$ was always obtained for variation between individuals.

The characteristic features of populational variation in *Drosophila* quantitative traits are as follows:

1. No spatial structure of the population is demonstrated (but it is not absent) with respect to any single trait, since the analysis of means revealed the variation of traits, while the place-time interaction was statistically significant for two traits.

2. A significant influence of sampling time was noted for three traits; however, the contribution of this factor was small (1.1-5.7%).

3. A place-time interaction could be established for the traits of wing length and thigh length, apparently due to a small residual variation; but its magnitude was small. The nature of this interaction is variable: It is both a multidirectional change in the ecological surroundings in time for different sampling sites and a diversity of norms of response of genotypes in space-time.

4. The uniqueness of a specific trait is manifested in the relationship of the two components of variation — that between individuals (at a given site and given collection time) and the residual variation. For traits channelized during ontogenesis, such as wing length and thigh length, the variation in trait values between the left and right of an individual is, of course, very small; therefore, the major variation is concentrated between individuals. For less channelized traits — the number of sternopleural and abdominal bristles and, especially, the number of arista hairs — the contribution of bilateral (metameric) variation is significantly greater, and therefore the variation between individuals is less.

Thus, the structure of intrapopulational variation is quite stable: If the contribution of spatial-temporal interactions is manifested in the general variation it does not exceed 6-10%.

We shall now examine only two components of variation — between individuals (σ_a^2) and within the individual (σ_e^2) — and we shall analyze the degree of stability of the estimate of the contribution of differences between individuals $r_w = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2)$ in space-time. The r_w values for samples of various volume were obtained in the following manner: 1) A sample of 125 individuals was taken, comprising females from sites 1-5 in sample A-80; 2) females from sites 6-10 in A-80 were added to the preceding sample; 3) females from sites 1-5 in S-80 were added to the preceding samples; ... 10) all individuals collected in the population. It was found that r_w with respect to the traits of wing length and thigh length differed by no more than 0.5%. The deviations were greater for the three other traits, comprising 4.1-9.3%. However, another fact is important: No r_w value exceeds the 95% confidence in-

terval constructed for the first sample, smallest in volume. Consequently, the contribution of the variation between individuals in the population is quite stable. Its significance, as stated above, consists in the sum of the genetic and ecological differences between individuals in the natural population.

The stability of variation in the territory studied by no means implies the genetic homogeneity of the population. Taylor and Powell (1977) collected *D. persimilis* in California in an area of about 700 × 800 m at six sites and twice a day at two sites. The sites differed in the frequencies of inversion in chromosome 2 and in the frequencies of alleles at nine enzymatic loci. Different frequencies of alleles in morning and evening samples were found at two loci. The variation between sampling sites comprised 5.4% of the total variation. Repeat samples of *D. willistoni* in Colombia were made in areas of several square meters (Hoenigsberg et al., 1977). The frequency of lethal and sublethal mutations differed in the dry and wet seasons; at the same time, during the dry season the frequencies in the course of the day varied from 11.3 to 25.6%. The spatial-temporal microgeographic variation in the animals may be associated with a genotypically conditioned preferential selection of habitat (Selander, 1970; Taylor and Powell, 1977). Microgeographic variation is well known in plant populations. It can be caused both by local variations in plant growing conditions (Hamrick and Holden, 1979; Shaw and Allard, 1981) and by a limitation of the radii of pollen and seed dispersal, as demonstrated on a computer model (Galitskii et al., 1983).

The quantitative traits of the plum *P. divaricata* were investigated on the Gunibskii Plateau (Dagestan ASSR) separately in two life forms – the single-stemmed tree and the shrub. Observations were made of 42 single-stemmed trees and 93 shrubs in the course of three years; moreover, the plants were not associated with one another by vegetative origin from a single source. Nine leaves were taken from each plant in each collection. The average values of the traits varied from year to year both in single-stemmed trees and in shrubs. Deviations from the overall variation for the different traits ranged from 4.8 to 17.2% during the three years; the most variable trait was "tooth number."

The overall variation was divided into two components – between individuals and within the individual – and the contribution between individuals (r_w) was separated. The reproducibility of the structure of intrapopulational variation is apparent in Table 2: Only for two pairs of observed quantities is the difference statistically significant at the 5% level (data on petiole length for single-stemmed tree are from 1981 and 1982; data on tooth number, from 1980 and 1982).

Since in contrast to the collections in the *Drosophila* population observations were made for the same subjects in the course of three years, the data can be analyzed in a two-factor system (model with random effects) after separating the individual-year interaction. The results of this analysis are presented in Table 3. The influence of year is small but significant in all cases except the vein number of the shrub. The influence of year for the "tooth number" trait is especially great; we recall that the average values of this trait were the most variable. The individual-year interaction proved especially great; it could reach 10-20%. However, a feature of the analytic scheme that might lead to an overestimate of the magnitude of interaction must be considered here. The analysis presumes a definite constancy of conditions in a given season for all individuals; at least they are more similar than conditions in different years. Considering the spatial microheterogeneity of the

TABLE 2. Contribution of Variation between Plum Plants, %

Trait	Life form								
	single-stemmed tree			shrub			shrub in thicket		
	1980	1981	1982	1980	1981	1982	1980	1981	1982
Petiole length	68,7±5,2	56,7±6,2	73,0±4,8	61,3±3,9	60,0±4,0	62,4±3,9	28,6±4,0	37,0±4,3	30,7±4,1
Leaf width	69,9±5,1	66,9±5,0	74,7±4,5	60,4±4,0	63,2±3,8	63,2±3,6	39,5±4,3	41,7±4,4	43,3±4,4
Vein number	35,3±6,3	32,5±6,2	25,8±5,7	27,4±3,9	37,5±4,2	30,6±4,0	4,7±2,1	7,2±2,4	2,2±1,8
Tooth number	58,8±6,0	49,3±6,4	42,7±6,5	38,9±4,3	42,9±3,7	42,5±3,7	14,3±3,1	18,2±3,4	12,2±2,9

TABLE 3. Structure of Variation of Plum in Two-Factor System (contribution of factors, %)

Trait	Life form							
	single-stemmed tree				shrub			
	plant	year	interac- tion	error	plant	year	interac- tion	error
Petiole length	54,4	4,6	9,4	31,6	49,2	1,4	11,3	38,1
Leaf width	55,0	2,1	14,8	28,1	39,0	1,9	12,1	37,0
Vein number	26,7	1,8	4,7	66,9	25,4	0,0	6,8	67,8
Tooth number	34,0	23,1	6,3	36,6	23,0	16,3	11,8	48,9

TABLE 4. Contributions of Variation between Plants for Single-Stemmed Plum Trees and Shrubs within Thicket, %

Trait	Single-stemmed trees	Shrubs (a)	Shrubs within thicket (b)	(b)/(a)
Petiole length	66,9	61,3	30,3	0,49
Leaf width	70,9	62,5	41,7	0,67
Vein number	30,9	32,7	4,7	0,15
Tooth number	51,4	41,4	15,1	0,36

habitat in highland Dagestan, it might be doubted that such constancy occurs. It is not ruled out that different individuals in a single season exist under substantially different habitat conditions. Therefore, it cannot be asserted that the observed interactions are due to a genotype-environment interaction. Rather, this is only partly true.

The role of ecological differences in the growing conditions of separate plants is well demonstrated by other data. For the shrub we were able to select 26 thickets with a total number of plants of 117; the number of plants in different thickets varied from 2 to 14. Insofar as plants within a thicket have an identical genotype, the differences between them are purely ecological. The overall variation was broken down into "between individual" and "within individual" components for each thicket separately, and then the estimates of variance were averaged. Table 2 presents the r_w estimates within the thickets during three years. It can be seen that they are well reproduced, as are the values for individual single-stemmed trees.

The r_w values within thickets averaged for three years were compared with the values for individual trees and shrubs (Table 4). The contribution of purely ecological variation within the variation between plants may reach half to two thirds. This gives a quantitative understanding of the complex ecogenetic nature of the differences between plants in the population during sexual reproduction. Thus, the relative stability of the intrapopulation structure of variation was also established for the plum.

Investigations devoted to the reproducibility of the structure of variation in natural populations are very few. Data on experimental, confined populations are very few. Data on experimental, confined populations can sometimes be used for *Drosophila* if the populations are not subjected to any manipulations and no artificial selection is performed. It is, of course, important that a sufficiently large number of individuals from the wild be used in organizing such populations. Extensive data on the reproducibility of estimates of inheritance ("progeny-parent" regression) in *D. melanogaster* were obtained in experiments on the study of genetic variation in a variable environment (Mackey, 1981). Two types of food were used, specified in a standard manner in the course of two years, while varying the cage in area as well as observing a definite cyclicity in time. Each experimental variant was conducted independently in two cages; the heritability with respect to the number of sternopleural and abdominal bristles and body weight was determined at the end of the first and second years of the experiment. The reproducibility of the estimate of heritability both in time and in repeat experiments was demonstrated in all variants.

The heritability of wing length was estimated in natural populations of *D. melanogaster* and *D. simulans* for half-sibs eight times in the course of two years (Tantawy, 1964). It proved stable for *D. simulans*. Similarly, low values (23 and 29%) were obtained during the

summer months in different years; in the remaining seasons the heritability was markedly higher (40-49%) but was also reproduced stably.

Three morphological traits were studied in *Musca domestica*: wing length, tibia length, and bristle length (Bryant, 1977). The material was collected monthly in Houston in the course of a year. It was found that the variation in different seasons comprised 24% of the total variation. However, this by no means indicates the poor reproducibility of the structure of variation. Data was gathered at nine sites in the USA for two years in a row during the same month. The exclusion of seasonal variation reduced the variation between samples in different years to only 2%.

The heritability ("progeny-parent" regression) of body weight and five size traits was estimated in the American song sparrow *Melospiza melodia* on an island in British Columbia for three years (Smith and Zach, 1979). Unfortunately, the authors present detailed data for only one year, but they note that the differences between estimates of heritability throughout the study period were statistically significant but small (not comparable with the differences for females and males) and not systematic. Apparently, the true magnitude of sampling error of heritability is greater than that usually calculated. Beak length and body length were compared in the same population for fledglings reared by their own (47 broods) and by adopted (40 broods) parents. A correspondence was demonstrated between traits of the progeny and those of the true parents (Smith and Dhondt, 1980).

Numerous examples of the reproducibility of the structure of variation can be found in international programs on forest amelioration (Wright, 1978). Campbell (1972) studied the annual growth of two-year Douglas-fir seedlings *Pseudotsuga menziesii* obtained in a scheme for crossing 63 trees from the population of the state of Washington. The parameters of heritability according to estimates in different years were 14.7 and 11.0%.

Thus, our own and published data indicate the adequate reproducibility of the structure of populational variation. Even the presence of the "genotype-environment" interaction, capable of altering the ranking of individuals by traits, has little influence on the estimates of the ecogenetic components of dispersion in simple experimental schemes. This makes it possible to analyze the population structure of the species according to separate samples and according to samples made in different years.

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