A NOTE ON THE ESTIMATION OF COMPONENTS OF VARIATION DUE TO INTERACTION BETWEEN GENOTYPE AND TEMPERATURE FOR WING LENGTH AND BRISTLE NUMBER IN *DROSOPHILA ANANASSAE*

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INTRODUCTION

The success of a breeder in improving a trait of economic importance depends on a precise estimate of the additive genetic variance for the trait present in the material under improvement. Various methods of estimation based on the resemblance between relatives like parent-offspring, half-sibs, full-sibs etc. are used but the data for the estimation are usually collected from material grown in only one stratum of the totality of environments for which the estimates are desired to apply. Such estimates are then confounded by variance arising from interactions of genotype and environment. Comstock (1960) studied the bias involved and concluded that data from an experiment conducted within a single stratum of environments cannot give conclusive information on the ratios of estimates of additive and dominance variance. It is thus apparent that in cases where the existence of interactions of genotype and environment is indicated, experiments need be conducted in more than one single stratum of environments. Taneja and Negi (1964) reported one such study in *Drosophila ananassae* and stressed the importance of these interactions. They used the method of sib analysis, raised the offspring from a sire-dam cross at two different temperatures and studied the characters wing length, bristle number and egg production. But they did not arrive at any estimates of the components of variance due to interaction of additive effects of genes and temperature or that due to interaction of dominance deviations and temperature, though this could have been done if the appropriate genetical model had been envisaged and the relation between this model and the statistical model used by them had been established. The object of this note is therefore to emphasise the genetical model inherent in their studies and obtain the estimates of components of variance due to interactions and the standard error of the estimates using their analysis of variance tables for the characters wing length and bristle number for either of the sexes.

STATISTICAL MODEL

The experimental design of Taneja and Negi (1964) consisted of mating each of 20 random males to a random sample of 2 virgin females, which were allowed to lay eggs separately. The larvae that emerged from each female's eggs which were full-sibs were divided randomly into two groups which were incubated at two different temperatures. A random sample of 8 progeny (4 males and 4 females) from a sire-dam cross for both the temperatures was considered for observation.

The analysis was performed on the basis of the following statistical model

$$y_{ijkl}=g+s_i+d_{ij}+t_k+(sd)t_{ijk}+e_{ijkl} \tag{1}$$

where y_{ijkl} is the lth observation ($l=1, 2$) in the kth treatment ($k=1, 2$) under the (ij)th cross ($i=1, 2\ldots20$ and $j=1, 2$), s_i is the random effect of ith sire with $E(s_i)=0$ and $V(s_i)=\sigma^2_s$, d_{ij} is the random effect of jth dam mated to ith sire with $E(d_{ij})=0$ and $V(d_{ij})=\sigma^2_d$, t_k is the random effect of the kth environment $E(t_k)=0$ and $V(t_k)=\sigma^2_t$, $(sd)t_{ijk}$ is the random interaction effect of (ij)th sire-dam cross with the kth environment $E(sd)t_{ijk}=0$ and $V(sd)t_{ijk}=\sigma^2_{sdt}$ and e_{ijkl} is the random error associated with y_{ijkl} with $E(e_{ijkl})=0$ and $V(e_{ijkl})=\sigma^2_e$. It is appropriate to call σ^2_s, σ^2_d, σ^2_t, σ^2_{sdt} and σ^2_e the observational components of the total variance, the term having been used by Falconer (1960) in sib-analysis within one macro-environment. The resulting analysis of variance for either of the sexes for wing length and bristle number along with the expectation of mean squares is reproduced in Table 1 from Taneja and Negi (1964). Equating the expectation of mean squares with their observed values, one can get the estimates σ^2_s, σ^2_d, σ^2_t, σ^2_{sdt} and σ^2_e.

Table 1. *Analysis of variance of wing length and bristle number of females and males (observed and expected values of mean squares)*

Source	d f	Wing length		Bristle number		Expectation of mean squares
		Females	Males	Females	Males	
Between sires	19	0·0007	0·0014	22·34	25·79	$\sigma^2_e+rt\,\sigma^2_d+rtd\,\sigma^2_s$
Between dams within sires	20	0·0012**	0·0009**	29·64	35·35**	$\sigma^2_e+rt\,\sigma^2_d$
Between temperatures	1	0·0580**	0·1100**	174·30**	99·00**	$\sigma^2_e+r\,\sigma^2_{sdt}+rds\,\sigma^2_t$
(Sire-dam) × temperature	39	0·0005**	0·0010**	20·47	23·36**	$\sigma^2_e+r\,\sigma^2_{sdt}$
Offspring within sire-dam × temperature	80	0·0002	0·0004	19·71	13·70	σ^2_e

N.B. **Significant at 1% level of significance.
r=2, s=20, d=2, t=2.

It is worth noting that the analysis of variance performed by Taneja and Negi (1964) would have been more informative if the source of variation due to sire-dam × temperature had further been split up into two more sources of variation viz. sire × temperature and dams within sires × temperature with 19 and 20 degrees of freedom respectively.

GENETICAL MODEL

The usual model for the phenotypic value P of an individual which is used in the study of the inheritance of characters showing continuous variation is given by

$$P=G+E \tag{2}$$

where G represents the genotypic value and E the environmental deviations. Mather and Jones (1958) modified it to include the interaction effects of G with E, where G

is assumed to be made up of additive effects of genes (breeding value) and the dominance deviations. Sarma and Narain (1965) extended the modified model to the case where G is assumed to include epistatic deviations also. However, in this study we will assume the model given by Mather and Jones (1958) since this leads to as many as five components of variation which is the maximum number capable of estimation in the design given by Taneja and Negi (1964).

Assuming a randomly breeding population, the total variance under the above model is given by:

$$V=\tfrac{1}{2}D+\tfrac{1}{4}H+\tfrac{1}{2}G_D+\tfrac{1}{4}G_H+E \tag{3}$$

where
$$D=4\sum_a p_a q_a[d_a+h_a(q_a-p_a)]^2$$
$$H=16\sum_a p^2{}_a q^2{}_a h^2{}_a$$
$$G_D=4\sum_a p_a q_a\, V[g_{da}+g_{ha}(q_a-p_a)]^2$$
$$G_H=16\sum_a p^2{}_a q^2{}_a\, V[g_{ha}]$$
$$E=V[e+\sum_a\{(p_a-q_a)g_{da}+2p_a q_a\, g_{ha}\}]$$

In the above expression p_a, q_a are the frequencies of alleles A and a respectively, d_a, h_a are the genetic effects as defined by Mather (1949) and g_{da} and g_{ha} are the interaction effects as defined by Mather and Jones (1958), e refers to the environmental comparison and $V[x]=\Sigma x^2$, summation being over the set of environments. When the sibs are distributed to the environments at random, the covariances between full-sibs and half-sibs are given by

$$Cov(F.S.)=\tfrac{1}{4}D+\tfrac{1}{16}H \tag{4}$$
$$Cov(H.S.)=\tfrac{1}{8}D \tag{5}$$

whereas when the environments of the sibs are always alike, these covariances are given by

$$Cov(F.S.)=\tfrac{1}{4}D+\tfrac{1}{16}H+\tfrac{1}{4}G_D+\tfrac{1}{16}G_H+E \tag{6}$$
$$Cov(H.S.)=\tfrac{1}{8}D+\tfrac{1}{8}G_D+E \tag{7}$$

Following Falconer (1960) we may term $\tfrac{1}{2}D$, $\tfrac{1}{4}H$, $\tfrac{1}{2}G_D$, $\tfrac{1}{4}G_H$ and E as the five causal components of total variance viz. additive genetic variance, dominance variance, variance due to interaction of additive effects and environment, variance due to dominance effects of genes and environment and environmental variance respectively.

RELATION BETWEEN THE OBSERVATIONAL AND CAUSAL COMPONENTS OF THE TOTAL VARIANCE

In the experiment reported by Taneja and Negi (1964) the two levels of temperature at which the offspring are raised can be regarded as providing two macro-environments for the genotype of each sire-dam cross. The group of full-sibs from each sire-dam cross is partitioned into parts and randomly allotted to the two macro-environments. Variance of the means of full-sib groups over the two temperatures, therefore, is $Cov(F.S.)$. In view of the statistical model (1), this variance is $\sigma^2{}_s+\sigma^2{}_d$. Hence, using (4),

$$\sigma^2{}_s+\sigma^2{}_d=\tfrac{1}{4}D+\tfrac{1}{16}H. \tag{8}$$

Similarly the variance of the mean of half-sib groups where a sire is common, is *Cov*(*H.S.*) and is $\sigma^2{}_s$ in terms of the statistical model, giving in view of (5), the relation

$$\sigma^2{}_s=\tfrac{1}{8}D. \tag{9}$$

Using (8) and (9)

$$\sigma^2{}_d=\tfrac{1}{8}D+\tfrac{1}{16}H. \tag{10}$$

When we consider the variance of the group of full-sibs without averaging over the two temperatures, we get *Cov*(*F.S.*), which by virtue of the statistical model, is $\sigma^2{}_s+\sigma^2{}_d+\sigma^2{}_t+\sigma^2{}_{sdt}$. Hence, using (6)

$$\sigma^2{}_s+\sigma^2{}_d+\sigma^2{}_t+\sigma^2{}_{sdt}=\tfrac{1}{4}D+\tfrac{1}{16}\,H+\tfrac{1}{4}\,G_D+\tfrac{1}{16}\,G_H+E. \tag{11}$$

Also, the variance of the means of temperatures is the observational component $\sigma^2{}_t$ on the one hand and is also the causal component E on the other hand. Hence

$$\sigma_t{}^2=E. \tag{12}$$

Using (8) and (12), (11) reduces to

$$\sigma^2{}_{sdt}=\tfrac{1}{4}G_D+\tfrac{1}{16}G_H. \tag{13}$$

Now $\sigma^2{}_e$ of the statistical model is the true variance between progenies within sire-dam cross × temperature. Assuming that the environmental differences can only be produced by variations in the temperature at which the flies are reared, $\sigma^2{}_e$ is $V-(\sigma^2{}_s+\sigma^2{}_d+\sigma^2{}_t+\sigma^2{}_{tdt})$. In view of (1) and (11) we therefore get

$$\sigma^2{}_e=\tfrac{1}{4}D+\tfrac{3}{16}H+\tfrac{1}{4}G_D+\tfrac{3}{16}G_H. \tag{14}$$

Thus (9), (10), (12), (13) and (14) establish the relations between the observational and causal components of the total variance. Putting the estimates of the observational components in these relations, we can solve for the five causal components.

STANDARD ERRORS OF THE COMPONENTS OF VARIANCE

Lee Crump (1946) has given a method of estimating the variance of any mean square, assuming that every component entering into the statistical model is a random one. Then each mean square is a χ^2 with the degrees of freedom associated with that mean square. Since the variance of χ^2 is $2f$ where f is the degrees of freedom, we have

$$V(\text{Mean square})=\frac{2}{f}\,(\text{Mean square})^2. \tag{15}$$

If we substitute estimated values of mean squares in this expression some bias is introduced. To correct this bias the following relation between the variance of the mean square and the mean square is used

$$V(\text{Mean square})=\frac{2}{f+2}\,(\text{Mean square})^2. \tag{16}$$

Now each component of the variance is ultimately expressed as a linear function of five independent mean squares so that the variance of the component of variance is simply a linear function of the variances of the mean squares. Using (16) to calculate the variance of each mean square involved, the desired variance of the component of variance is calculated. Each component of variance is then tested by the usual *t*-test. The number of degrees of freedom to be used for the test is however obtained by the method given by Sttarthwaite (1946). Let

$$V_s=a_1\,MS_1+a_2\,MS_2+\,\ldots, \tag{17}$$

where a_1, a_2 etc. are some constants. The number of degrees of freedom f_s of the approximating χ^2 is found to be

$$f_s = \frac{[a_1 E(MS_1) + a_2 E(MS_2) + \dots]^2}{\dfrac{[a_1\, E(MS_1)]^2}{f_1} + \dfrac{[a_2 E(MS_2)]^2 \dots}{f_2}}, \tag{18}$$

where E denotes expectation and f_1 denotes the degrees of freedom of MS_1. In the above expression, the expected values of mean squares are replaced by their observed values in actual computation. However, some care is necessary in using this approximation. Since χ^2 does not take negative values, if any component comes out to be negative, we cannot obtain the number of degrees of freedom.

RESULTS

The above considerations have been applied to the mean squares given in Table 1 for the characters wing length and bristle number for each sex. The results obtained are given in Tables 2 and 3.

Table 2. *Estimates of the components of variance with their standard errors and their contributions to the total variance for wing length*

Components	Females			Males		
	Estimate	Standard error	Contribution to total variance	Estimate	Standard error	Contribution to total variance
$\frac{D}{2}$	0·000000	0·00021348	0·0000	0·00025000	0·00025509	0·0934
$\frac{H}{4}$	0·0012500*	0·00055532	0·4123	0·00025000	0·00046500	0·0934
$\frac{G_D}{2}$	0·0010625**	0·00036786	0·3505	0·00081250*	0·00031701	0·3036
$\frac{G_H}{4}$	0·0000000	0·00064660	0·0000	0·00000000	0·00060410	0·0000
E	0·0007188	0·00030330	0·2371	0·00136375	0·00112280	0·5096

*Significance at 5% level of probability
**Significance at 1% level of probability

For the character wing length in females, components H and G_D are found to be significant; their relative contributions to the variance being 41% and 35% respectively. In males for this character, G_D is the only component which is found to be significant accounting for about 30% of the total variation. For the character bristle number, however, none of the components is found to be significant in either of the sexes.

It is, therefore, concluded from these results that the macro-environment, which is temperature in this study, interacts with the additive effects of genes for the character wing length in either of the sexes, but no interactions are found significant for the

Table 3. *Estimates of the components of variance with their standard errors and their contributions to the total variance for bristle number*

Components	Females			Males		
	Estimate	Standard error	Contribution to total variance	Estimate	Standard error	Contribution to total variance
$\frac{D}{2}$	0·000000	6·3900	0·0000	0·0000	6·76500	0·0000
$\frac{H}{4}$	8·730000	14·4925	0·2536	21·7700	16·16500	0·5389
$\frac{G_D}{2}$	0·000000	14·4200	0·0000	17·6775	14·01000	0·4376
$\frac{G_H}{4}$	23·76500	21·2725	0·6905	0·0000	21·70875	0·0000
E	1·922875	1·7778	0·0558	0·9455	1·01080	0·0234

character bristle number. The analysis made by Taneja and Negi (1964) however, did not go deeper to find out the nature of genotype × environment interaction, though they reported their significance for wing length in either sexes and for bristle number in male sex. By means of the procedure followed and reported in this paper it is apparent that the experiment reported by them can lead to more information in respect of the nature of the genotype × environment interactions and their estimates.

SUMMARY

The analysis of the experiment conducted by Taneja and Negi (1964) in respect of genotype × temperature interactions in *Drosophila ananassae* has been examined critically by emphasising the underlying genetical model and the estimates of the component variation along with their standard errors have been obtained afresh.

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