HERITABILITY OF A RESPONSE TO AN ENVIRONMENTAL CHANGE IN CHICKENS¹

WALTER A. BECKER

Washington State University, Pullman

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THE response of an individual within a species to changes in the environment depends upon the genotype and developmental history of the organism. WADDINGTON (1957) has designated the selection of genotypes which resist changes in the environment as "canalizing selection" and has provided an example of this type of selection when he (1960) practiced family selection for reduced environmental sensitivity of the number of eye facets in a Bar mutant *Drosophila* stock to the temperatures 18° and 25°C. Selection was effective in reducing the difference about 10 percent between the two temperature environments in five generations.

This reduction occurred in a selected population which was abnormal in that the population included a dominant mutant gene, Bar. If this canalizing selection phenomenon has general applicability, then it should be possible to measure the genetic variation of the response of a nonmutant population to an environmental change. To examine this point, a random-bred population of pedigreed chickens was divided and each half was placed in different nutritional environments, and the body weights measured. Estimates were made of the heritabilities of the response to this environmental change, as well as the genetic correlations between environments.

EXPERIMENTAL DESIGN

Six hundred White Leghorn pullets were single-sire mated, in groups of 15 dams, to 40 sires. Both came from a population which had been random mated for 13 generations. Eggs were pedigreed and set in a series of three hatches, one week apart, to provide the chicks. In all, 4,580 were hatched for the study. In each hatch, every chick was banded and identified as to its sire and dam. One half of the progeny of each dam's family was randomly assigned to one of two environments. Within each pair of environments there were two pens to which animals were randomly distributed. The chicks were fed a nutritionally adequate ration that was in a pelleted form (superior environment), or in a mash condition (inferior environment).

The 2,724 males were weighed at 4 weeks of age to the nearest gram and were then removed. Soon after this weighing, the usefulness of the second hatch of females was destroyed by an unfortunate occurrence of vandalism and, therefore, only the first and third hatches, 1,856 females in all, were weighed when 8 weeks old.

In the analysis of the data, an additive correction was made to the weights of the animals in the third hatch because there were pen effects within environments. The individual data for each sex within each diet were analyzed in a double-nested analysis of variance design to obtain estimates of genetic, environmental and phenotypic variances which were used to compute

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TABLE 1

Analysis of variance table illustrating the composition of expected mean squares using individual progeny weights

Source of variation	EMS
Between sires	$\sigma_w^2 + k_2 \sigma_D^2 + k_3 \sigma_s^2$
Between dams, within sires	$\sigma_w^2 + k_1 \sigma_D^2$
Between individual progeny, within dams	σ_w^2

TABLE 2

Composition of expected mean squares and mean cross products when means of each dam's progeny were used

Source of variation	EMS	EMCP
Between sires	$\left(\frac{\sigma_w^2}{k_1} + \sigma_D^2 \right) + k_2 \sigma_s^2$	$\left(\frac{Cov_W}{k_1} + Cov_D \right) + k_2 Cov_s$
Between dams, within sires	$\left(\frac{\sigma_w^2}{k_1} + \sigma_D^2 \right)$	$\left(\frac{Cov_W}{k_1} + Cov_D \right)$

k_1 = number of progeny per dam. k_2 = number of dams per sire. σ_s^2 = sire component. σ_D^2 = dam component. σ_w^2 = individual's component. Cov = covariance.

the heritabilities of body weight. Table 1 gives the composition of the expected mean squares of this design. The coefficients were calculated for unequal numbers per cell as given by ANDERSON and BANCROFT (1952).

For the analyses involving the relationship between the two environments, the mean of each dam's progeny in each environment was used as the observation. Table 2 shows the composition of the expected mean squares and mean cross products (EMCP) when the average of the offspring of each dam was used as the observation in the analysis of variance. Within each sex, the response to the environmental change was determined for each dam's progeny by subtracting the mean of the progeny on the inferior diet from the mean of the progeny fed the superior diet. This figure then was used as a basis for estimating the genetic variance and heritability of the response to an environmental change.

The justification for the classification of the environments as superior and inferior is presented in Table 3, where the 4-week old males weighed 283 grams in the superior environment and 236 g in the inferior environment. The 8-week females weighed 680 g when fed the pelleted ration and 585 g when given the mash feed.

The data were analyzed in the same manner using the logarithmic transformation but, because this transformation did not produce different results than when the arithmetic scale was used, only the latter scale will be presented.

RESULTS

The means, the sire component, σ_s^2 , which estimates 1/4 the additive genetic variance and 1/16 of the additive $\times$ additive genetic variance, the dam component, σ_D^2 , which estimates 1/4 the additive genetic variance, 1/4 the dominance variance, all the maternal effects variance and various amounts of epistatic variance, are given in Table 3 along with the variance, σ_w^2 , attributable to the differ-

TABLE 3

Means, variance components and heritabilities of individual males and females on two diets

Estimate	Environments			
	4-week males		8-week females	
	Superior	Inferior	Superior	Inferior
$\bar{x}$ (grams)	283	236	680	585
σ_s^2	88	78	855	636
σ_D^2	254	19	808	1,187
σ_W^2	875	1,339	3,486	4,387
σ_P^2	1,217	1,436	5,149	6,210
h_s^2	0.29 $\pm$ 0.63 0.21 $\pm$ 0.44		0.66 $\pm$ 0.93 0.41 $\pm$ 0.68	

$$\sigma_P^2 = \sigma_W^2 + \sigma_s^2 + \sigma_D^2$$

$$h_s^2 = 4 \sigma_s^2 / \sigma_P^2$$

ences between full sib progenies within dam families. The phenotypic variance and the estimates of the heritabilities with their standard errors are presented.

The difference between environments, as measured by the means of each sex, was 47 g for the 4-week old males and 95 g for the 8-week old females. The phenotypic variances differed depending upon the environment in which the animals were developed, being larger when the birds were in the inferior environment than when they were raised in the superior environment.

The magnitude of the standard errors of the heritabilities makes it difficult to infer from the data that any differences of the estimates of heritabilities are attributable to the environment in which the birds are raised.

The estimate of the dam's component for the 4-week old males is inconsistent with the other estimates, but a careful check did not reveal any definite reasons for this low estimate.

The mean of each dam's offspring on the superior environment minus the mean of those on the inferior environment was designated as the population's response to the environmental change ($\bar{x}_1 - \bar{x}_2$).

The variance of a difference is

$$\sigma_{(1-2)}^2 = \sigma_1^2 + \sigma_2^2 - 2 \text{Cov}_{(12)} \quad (1)$$

so that the variance of a difference of the mean substituting from the expected mean squares as given in Table 2 for the between dams, within sires mean square would be

$$\sigma_D^2 = \sigma_{D_1}^2 + \frac{\sigma_{W_1}^2}{k_1} + \sigma_{D_2}^2 + \frac{\sigma_{W_2}^2}{k_2} - 2\rho(\bar{x}_1 \bar{x}_2) \sqrt{(\sigma_{D_1}^2 + \frac{\sigma_{W_1}^2}{k_1})(\sigma_{D_2}^2 + \frac{\sigma_{W_2}^2}{k_2})} \quad (2)$$

where D and W have the same meaning as in Table 2, 1 = superior and 2 = inferior environments, and k is the number of progeny of each dam in each environment.

The heritability of the response was computed by

$$h_s^2 = \frac{4 \sigma_s^2}{\sigma_s^2 + \sigma_D^2} \quad (3)$$

TABLE 4

Variance components and heritabilities of the difference between dam's means of progeny on two diets ($\bar{x}_1 - \bar{x}_2$)

Age and sex	$\hat{\sigma}_s^2$	$\hat{\sigma}_D^2$	h_s^2
4-week males	55	1,019	0.20 ± 0.42
8-weeks females	303	4,568	0.25 ± 0.46

TABLE 5

The estimates of the components of variance and covariance obtained from the means of the progeny of each dam

Components	Variances in inferior environment		Covariance between environments		Variances in superior environment	
	Males	Females	Males	Females	Males	Females
Sires	89.5	807	63.2	643	92.3	783
Dams	657	3,530	163	851	688	2,740

This estimate is a heritability of the mean differences and is given for both sexes in Table 4 along with estimates of the components. The heritability of this response was 0.20 for males and 0.25 for females. If this heritability had been computed from individual data the estimates would have been less.

The genetic correlation between environments was computed by the analysis of covariance where

$$r_G(\bar{x}_1, \bar{x}_2) = \frac{Cov_S(\bar{x}_1, \bar{x}_2)}{\sigma_{S_1} \sigma_{S_2}} \quad (4)$$

The estimates of the various components of variance and covariance are presented in Table 5. The genetic correlations between environments were 0.70 for the males and 0.81 for the females.

The phenotypic correlation, r_{P_w} , between environments, within sire groups can be estimated from formula (2) where $\rho(\bar{x}_1, \bar{x}_2) = r_{P_w}$.

$$r_{P_w} = \frac{\frac{\sigma_{D_1}^2 + \sigma_{w_1}^2}{k_1} + \frac{\sigma_{D_2}^2 + \sigma_{w_2}^2}{k_2} - \sigma_D^2}{2 \sqrt{(\sigma_{D_1}^2 + \frac{\sigma_{w_1}^2}{k_1})(\sigma_{D_2}^2 + \frac{\sigma_{w_2}^2}{k_2})}} \quad (5)$$

This correlation is expected to be different from r_G (ROBERTSON 1959) and would be greatly affected by maternal effects influencing the σ_D^2 's.

The estimates of this correlation were 0.242 for males and 0.274 for females, using data from Tables 4 and 5. Estimates of the genetic correlation between environments can be obtained by solving as follows:

$$r_{G(x_1 x_2)} = \frac{r_{P_w}}{\frac{h_1}{2} \sqrt{\frac{k_1}{1+(k_1-1)t_1}} \frac{h_2}{2} \sqrt{\frac{k_2}{1+(k_2-1)t_2}}} \quad (6)$$

This formula is given by TOUCHBERRY, ROTTENSTEN and ANDERSON (1960), where the h 's refer to the square root of the heritabilities on an individual basis and the t 's are the intra-class correlation coefficients associated with the dams. The genetic correlations were obtained using data from Table 3 and the estimates of the phenotypic correlation within sires. The genetic correlations were 2.55 for the 4-week males and 0.993 for the 8-week females.

DISCUSSION AND CONCLUSIONS

Several instances of increased phenotypic variances of animals in environments which may be considered "sub-optimal" have been reviewed by BIGGERS, McLAREN and MICHIE (1958). A similar situation was reported by BECKER and BERG (1959), although MERRITT, DOWNS, BORDEAU and TINNEY (1960) in a similar experiment failed to obtain an increased variance when chickens were placed in an inferior environment. BOWMAN and POWELL (1962), working with chickens, have found that the between-variety genetic variance remained constant while the within-variety variance decreased when the environment was improved.

Even though the heritability may be increased by shifting to another environment, this does not necessarily mean genetic progress within that environment would be greater than progress within another environment if an artificial selection program were initiated. If the phenotypic variance is larger in one environment than in another, the selection differential of animals in the environment with the increased variance would be expected to be greater than the selection differential in the other environment. Therefore, even though the heritabilities differed, the genetic progress could be the same in each environment.

The experimental results indicated that there was additive genetic variance of the response to this specific environmental change. It is suggested that selection for decreased sensitivity to certain environments might be utilized in domesticated species to develop strains resistant to specific environmental stresses. Placing the progeny of each sire in each environment and selecting on a sire family basis for a small difference between environments should produce a genetic change in the response to the two environments. Conversely, stocks of laboratory animals might be developed by artificial selection which would be sensitive to certain environmental changes.

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SUMMARY

Progeny of 40 White Leghorn sires and 600 dams were randomly allotted when hatched to two dietary environments, one a low energy mash ration (inferior environment) and the other the same formula in a pelleted form (superior environment).

For 4-week old males in the inferior environment: $N = 1,217$, $\bar{x} = 235$ grams; phenotypic variance = 1,436, $h_s^2 = 0.21 \pm 0.44$. Results in superior environment: $N = 1,507$, $\bar{x} = 283$ grams, phenotypic variance = 1,217, $h_s^2 = 0.29 \pm 0.63$. The genetic correlation between environments was 0.70 and the heritability of the response measured as the difference between means of dam's progeny in both environment, was $h_s^2 = 0.20$. Data on 8-week females fed the inferior diet were: $N = 936$, $\bar{x} = 585$ g, phenotypic variance = 6,210, $h_s^2 = 0.41 \pm 0.68$. Results for animals fed a superior diet: $N = 920$, $\bar{x} = 680$ g, phenotypic variance = 5,149, $h_s^2 = 0.66 \pm 0.93$. The genetic correlation between environments was 0.81 and the heritability of the response was $h_s^2 = 0.25$. The use of the logarithmic transformation did not significantly alter the results. It is suggested that strains of laboratory animals presumably could be selected for sensitivity to certain drugs and that domesticated animals might be selected for resistance to specific environmental stresses.

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