

Genotype – Hatch Interactions as a Source of Bias in Estimating Genetic Components of Variance for Eight-Week Weight in Poultry¹

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Summary. Data on 16,557 chicks from 198 sire groups were analyzed to determine the importance of genotype-hatch interactions as sources of bias in the estimation of genetic parameters for eight-week weight in poultry. Estimates of heritability for eight-week weight obtained from a paternal half-sib correlation were $.27 \pm .04$ and $.29 \pm .04$ for males and females respectively when the sire component of variance was unconfounded with the sire-hatch interaction variance. If the sire-hatch interaction effects were confounded with the sire effects in an intra-hatch analysis the corresponding estimates of heritability would be .30 and .35 for males and females respectively. No attempt was made to artificially create differences in the hatch environments.

The ratio of the dam-hatch interaction variance to the dam component of variance as compared with the sire-hatch interaction variance to the sire component gave a slight indication of a greater degree of importance of the interaction of non-additive genetic-environment effects than additive \times environmental effects in the male progeny but not in the female progeny.

Introduction

Several experiments have been reported in the literature that have evaluated the predictability of short term response to selection in both large animals and laboratory populations. (CLAYTON *et al.*, 1957; RAHNEFELD *et al.*, 1963; MARTIN and BELL, 1960; ENFIELD *et al.*, 1966; HETZER and HARVEY, 1967 and SIEGEL, 1962, are among the many that might be cited.) In such experiments it is often observed that the actual response to selection falls short of that predicted based on estimates of appropriate genetic parameters in the corresponding populations. One of the more commonly used methods of estimating heritability for predictive purposes is the intra-class correlation where the sire component of variance estimated from a nested-classification (see KING and HENDERSON, 1954) for a given sub-set of environments provides an estimate of one-fourth the additive genetic variance. Such estimates of sire components are often made on an intra-time period analysis, i. e. within years, generations, cycles, etc. For the sire component to be an unbiased estimator of additive genetic variance in such an analysis the given time periods must either be representative of the totality of environments to which the estimate has application or there must be no genotype-environmental interaction. A sire-environment interaction effect in such an analysis is confounded with the sire effect and thus can bias upward the estimate of additive genetic variance.

Several experiments have been reported in the literature which have been designed to evaluate the

importance of genotype-environment interactions (ABPLANALP, 1956; BRADFORD, 1968; HARDIN *et al.*, 1967; DICKERSON, 1962 serve as examples). Several of these experiments have shown that such interactions may be important sources of variation especially when sharply different environments are imposed.

From the standpoint of parameter estimation one of the questions raised is how much bias is involved in estimation of genetic parameters on a within time-space basis when no attempt is made to create major differences in macro-environments over a period of generations. The theoretical issues related to this problem have been examined by COMSTOCK (1960), COMSTOCK and MOLL (1963) and FALCONER (1952).

The emphasis in this paper is to assess the magnitude of genotype-hatch interactions for eight-week weight in two broiler populations of poultry and to determine the extent of bias in heritability estimates when the data are analyzed on a within-hatch basis where hatch differences are considered random relative to the total population of macro-environments.

Materials and Methods

The data for this project were collected over a two year period with ten separate hatches represented. Two broiler strains are represented in the analysis. Strain A was largely a New Hampshire Red strain with some introduction of outside blood for the purpose of bringing the dominant white gene into the population. Strain B was primarily of Rhode Island Red breeding but introductions from outside sources had been made. The amount of data represented in each hatch and the breeding of the chicks involved are given in Table 1. Male and female eight-week weight were treated as different traits and thus were analyzed separately.

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Table 1. Numbers of sires, dams, and progeny in each hatch

Hatch code	Breeding	No. of sires	No. of dams	No. of male progeny	No. of female progeny
169	Strain B	36	190	752	695
173				629	631
177	B	27	151	538	567
178				486	540
215	B	55	252	966	1009
227				846	950
233	B	51	313	1076	1113
238				1081	1123
238	A	29	205	898	914
246				871	872
Total		198	1111	8143	8414

The experimental plan was such that progenies from a given set of matings were represented in two separate hatches. The statistical model employed and the expectations of the analysis of variance are given in Table 2. In this analysis the statistical unit consisted of a full-sib family mean for a given hatch. A second analysis was used on a smaller segment of the data where the experimental unit was an individual observation so that an estimate of the within-full-sib family component could be obtained.

Two issues are considered pertinent in the analysis. The first concerns the magnitude of the estimate of the sire-hatch interaction ($\hat{\sigma}_{st}^2$) relative to the sire component estimate ($\hat{\sigma}_s^2$). In this case we are considering the importance of the interaction of additive gene effects with environment and the potential bias associated with estimates of additive genetic variance and heritability in the narrow sense obtained from an intra-hatch analysis. The second issue is the one identified by COMSTOCK (1960) in discussion of the magnitude of genotype-environment interaction variances relative to associated kinds of genetic variance as a potential source of bias in estimation of relative magnitude of dominance and additive variance. Although the evidence is complicated with maternal effects in this data the ratio $\hat{\sigma}_{dt}^2/\hat{\sigma}_d^2$ as compared with $\hat{\sigma}_{st}^2/\hat{\sigma}_s^2$ will provide some information on this matter.

Results and Discussion

The estimated components of variance for male and female eight-week weight are given in Tables 3 and 4. These components are expressed as a percent of the total phenotypic variance in Table 5.

The pooled estimates of heritability obtained for the ratio, $4\hat{\sigma}_s^2/\hat{\sigma}_p^2$, of $.27 \pm .04$ and $.29 \pm .04$ for males and females respectively are lower than the median of the estimates for this trait reported in the literature as summarized by SIEGEL (1962). If the sire-hatch interaction effect were confounded with the sire effects heritability would be estimated from the ratio $4(\hat{\sigma}_s^2 + \hat{\sigma}_{st}^2)/\hat{\sigma}_p^2$ in an intra-hatch analysis. These estimates of heritability would be .30 and .35 for males and females respectively. Standard errors were large enough so that upward bias may have been moderately larger than actually estimated. However, the results of this study add to the weight of evidence reported by other workers, indicating

Table 2. Analysis of Variance and Expected Mean Squares

Model $\bar{P}_{ijk} = \mu + s_i + d_{ij} + t_k + (st)_{ik} + (dt)_{ijk} + \frac{1}{n_{ijk}} \sum e_{ijkl}$

(complete random model)

where: \bar{P}_{ijk} = the family mean for the k^{th} hatch from the j^{th} dam mated to the i^{th} sire.
 μ = general mean for the measurement.
 s_i = an effect common to all individuals from the i^{th} sire.
 d_{ij} = an effect common to all individuals from the j^{th} dam mated to the i^{th} sire.
 t_k = an effect common to all individuals in the k^{th} hatch.
 $(st)_{ik}$ = an interaction effect between sire and hatch common to all individuals from the i^{th} sire in the k^{th} hatch.
 $(dt)_{ijk}$ = an interaction effect between dam and hatch common to all individuals from the j^{th} dam mated to the i^{th} sire in the k^{th} hatch.
 e_{ijkl} = a residual effect on phenotype of the l^{th} individual in the k^{th} hatch from the j^{th} dam mated to the i^{th} sire.
 n_{ijk} = the number of individuals from the j^{th} dam mated to the i^{th} sire in the k^{th} hatch.

Variance Sources	Degrees of Freedom	Expected Mean Squares
Between hatches	$k - 1$	
Among sires	$s - 1$	$k_2 \sigma_s^2 + \sigma_{dt}^2 + k_3 \sigma_{st}^2 + k \sigma_d^2 + k_4 \sigma_s^2$
Among dams within sires	$\sum_i n_i - s$	$k_1 \sigma_s^2 + \sigma_{dt}^2 + k \sigma_d^2$
Hatch x sire	$(k - 1)(s - 1)$	$k_2 \sigma_s^2 + \sigma_{dt}^2 + k_3 \sigma_{st}^2$
Hatch x dams within sires	$(k - 1)(\sum_i n_i - s)$	$k_1 \sigma_s^2 + \sigma_{dt}^2$

Table 2. (con't.) Analysis of Variance and Expected Mean Squares

$k_1 = \frac{1}{\sum_i n_i - s} \frac{(1)}{k} \left(\sum_i \sum_j \sum_k \frac{1}{n_{ijk}} - \sum_i \frac{1}{n_i} \sum_j \sum_k \frac{1}{n_{ijk}} \right)$

$k_2 = \frac{1}{(s - 1)k} \left(\sum_i \frac{1}{n_i} \sum_j \sum_k \frac{1}{n_{ijk}} - \frac{1}{\sum_i n_i} \sum_i \sum_j \sum_k \frac{1}{n_{ijk}} \right)$

$k_3 = \frac{1}{s - 1} \left(\sum_i n_i - \frac{\sum_i n_i^2}{\sum_i n_i} \right)$

$k_4 = \frac{k}{s - 1} \left(\sum_i n_i - \frac{\sum_i n_i^2}{\sum_i n_i} \right)$

k = number of hatches
 s = number of sires
 n_{ijk} = number of offspring per dam in the k^{th} hatch
 n_i = number of dams mated to the i^{th} sire
 $\sum_i n_i$ = total number of dams
 N = total number of dam hatch subclasses

Table 3. *Components of Variance and Estimates of Heritability for Eight-Week Weight in Males*

Hatches	Breeding	$\hat{\sigma}_e^2$	$\hat{\sigma}_{dt}^2$	$\hat{\sigma}_{st}^2$	$\hat{\sigma}_d^2$	$\hat{\sigma}_s^2$	Heritability*
238, 246	Line A	.0540	.0123	-.0027	.0046	.0069	.35
169, 173	Line B	.0238	.0081	-.0005	.0040	.0025	.26
215, 227	Line B	.0373	-.0007	.0021	.0110	.0018	.14
177, 178	Line B	.0480	.0079	.0007	.0038	.0049	.30
233, 238	Line B	.0440	-.0038	.0005	.0086	.0044	.31
Pooled	Line A and B	.0411	.0036	.0003	.0080	.0039	.27
		$\pm .0051$	$\pm .0030$	$\pm .0008$	$\pm .0014$	$\pm .0009$	$\pm .04$

* $4 \sigma_s^2 / \sigma_p^2$ where σ_p^2 is the sum of the within hatch components variance.

Table 4. *Components of Variance and Estimates of Heritability for Eight-Week Weight in Females*

Hatches	Breeding	$\hat{\sigma}_e^2$	$\hat{\sigma}_{dt}^2$	$\hat{\sigma}_{st}^2$	$\hat{\sigma}_d^2$	$\hat{\sigma}_s^2$	Heritability
238, 246	Line A	.0203	.0035	.0018	.0069	.0049	.52
169, 173	Line B	.0235	.0004	.0004	.0054	.0028	.34
177, 178	Line B	.0317	-.0002	.0008	.0053	.0017	.17
215, 227	Line B	.0264	.0008	.0001	.0040	.0020	.24
233, 238	Line B	.0246	.0001	.0001	.0050	.0021	.26
Pooled	Line A and B	.0256	.0006	.0005	.0053	.0025	.29
		$\pm .0019$	$\pm .0007$	$\pm .0003$	$\pm .0005$	$\pm .0006$	$\pm .04$

that over normal variations in environment, variance due to interaction of genotype and environment is quite small relative to genetic variance.

ABPLANALP (1956) considered the importance of hatch \times sire interaction effects for a number of different egg production traits in a flock maintained by Kimber Farms, Niles, California. His conclusion was that genotype-environmental interactions contribute relatively little to total variation and may be of negligible magnitude. However, in his study in the case of data related to age at first egg the hatch \times sire component was nearly twice the magnitude of the sire component itself which in this instance would have resulted in a considerable upward bias in the estimation of heritability on an intra-hatch basis. In other data of this kind JOHNSON and ASMUNDSON (1957) found a significant sire \times hatch interaction for eight-week weight in turkeys when data were included from hatches where the brooding temperatures had been abnormally high. In hatches of normal temperature no interaction effects were noted. GOODWIN and DICKERSON (1956) and GOWE (1956) were interested in determining whether genotype \times location interactions were an important source of variation for broiler traits. No significant interaction effects were found for early growth rate in either study.

COMSTOCK and MOLL (1963) discuss the potential biases associated with estimates of genetic variance components obtained from data collected in a single macro-environment, i. e. hatches, years, locations, etc. If the variance estimates are to be used in the form of ratios for such purposes as estimating level of dominance (see MOLL *et al.*, 1964; ENFIELD *et al.*, 1969) then the issue of whether the biases associated with genotype-environment interactions have the

Table 5. *Per Cent of the Total Variation in Eight-Week Weight Attributed to the Various Components*

Sex	Hatch	Line	Components of Variance (% of total variance)				
			$\hat{\sigma}_e^2$	$\hat{\sigma}_{dt}^2$	$\hat{\sigma}_{st}^2$	$\hat{\sigma}_d^2$	$\hat{\sigma}_s^2$
Males	238 246	A	69.41	15.81	*	5.91	8.87
		B	61.98	21.09	*	10.42	6.51
	215 227	B	71.46	*	4.02	21.07	3.45
		B	73.51	12.10	1.07	5.82	7.50
	233 238	B	76.52	*	.87	14.96	7.65
		Pooled	A & B	74.47	3.44	.54	14.49
Females	238 246	A	54.28	9.36	4.81	18.45	13.10
		B	72.30	1.23	1.23	16.62	8.62
	177 178	B	80.25	*	2.03	13.42	4.30
		B	79.28	2.40	.30	12.01	6.01
	233 238	B	77.12	.31	.31	15.67	6.58
		Pooled	A & B	74.21	1.74	1.45	15.36

* indicates a negative estimate

same ratios as the true genetic variances is of interest. This issue can be evaluated in the present study by comparing the ratios, $\hat{\sigma}_{dt}^2 / \hat{\sigma}_d^2$ with $\hat{\sigma}_{st}^2 / \hat{\sigma}_s^2$. If dominance variance is an important source of variation then $\hat{\sigma}_d^2 > \hat{\sigma}_s^2$. In both the male and female data the magnitude of $\hat{\sigma}_d^2$ is approximately double $\hat{\sigma}_s^2$. This may be due only in part to dominance variance with maternal

effects also likely to be contributing to $\hat{\sigma}_d^2$. The ratios of the interaction variances to their corresponding sire or dam components are as follows:

	$\hat{\sigma}_{di}^2/\hat{\sigma}_d^2$	$\hat{\sigma}_{si}^2/\hat{\sigma}_s^2$
Male progeny	.45	.07
Female progeny	.11	.20

In the female progeny data there is nothing to indicate differences in importance of interaction of kinds of genetic effects with environment. In the male progeny data there is some indication that the interaction of non-additive genetic effects with environment is of a higher order of magnitude than the additive \times environmental effects. However the large sampling errors associated with the ratio preclude the observed differences being statistically significant. The relative importance of the interaction of environment with additive and non-additive genetic effects has been considered in some plant breeding experiments where genotype-environment interactions are considered more important sources of variation. ROJAS and SPRAGUE (1952) reported that in the case of corn yield the interaction variance associated with dominance effects was larger relative to dominance variance than interaction variance associated with additive effects relative to additive genetic variance. Conflicting results were reported by COMSTOCK (1960) for the same trait. However, in both experiments the relative magnitude of the interaction variances to the genetic variances was much larger than our data indicates for eight-week weight in poultry.

The results of this study suggest that when no attempt is made to create environmental differences between hatches, the interaction of genotype with the random environmental effects associated with differences among hatches contribute a relatively small fraction (less than 4%) of the total variation for eight-week weight in poultry. Estimates of additive genetic variance and heritability estimated on an intra-hatch basis would be biased upward 10 to 20 per cent when considering eight-week weight.

Literature Cited

1. ABPLANALP, HANS: Selection procedures for poultry flocks with many hatches. *Poultry Sci.* **35**, 1285—1304 (1956).
2. BRADFORD, G. E.: Selection for litter size in mice in the presence and absence of gonadotropic treatment. *Genetics* **58**, 283—295 (1968).
3. CLAYTON, G. A., J. A. MORRIS and ALAN ROBERTSON: An experimental check on quantitative genetic theory. I. Short term responses to selection. *J. of Genetics* **55**, 131—151 (1957).
4. COMSTOCK, R. E.: Dominance, genotype-environment interaction, and homeostasis. In: *Biometrical Genetics*, edited by O. KEMPTHORNE, pp. 3—9. New York: Pergamon Press 1960.
5. COMSTOCK, R. E., and R. H. MOLL: Genotype-environment interactions. In: *Statistical Genetics and Plant Breeding*, pp. 164—196. NAS-NRC 982 (1963).
6. DICKERSON, G. E.: Implications of genetic-environmental interactions in animal breeding. *Animal Prod.* **4**, 47—63 (1962).
7. ENFIELD, F. D., R. E. COMSTOCK, and O. BRASKERUD: Selection for pupa weight in *Tribolium castaneum*. I. Parameters in base populations. *Genetics* **54**, 523—533 (1966).
8. ENFIELD, F. D., R. E. COMSTOCK, ROBERT GOODWILL and O. BRASKERUD: Selection for pupa weight in *Tribolium castaneum*. II. Linkage and level of dominance. *Genetics* **62**, 849 to 857 (1969).
9. FALCONER, D. S.: The problem of environment and selection. *Amer. Nat.* **86**, 293—298 (1952).
10. GOODWIN, K., and G. E. DICKERSON: A test of cross \times location interactions for five traits in fryers. *Proc. Ninth Pacific Coast Chicken and Turkey Breeders Roundtable* **9**, 54—60 (1956).
11. GOWE, R. S.: Performance of many strains and crosses kept at many stations in Canada. *Proc. Ninth Pacific Coast Chicken and Turkey Breeders Roundtable* **9**, 40—54 (1956).
12. HARDIN, R. T., J. C. ROGLER, and A. E. BELL: Genetic and environmental interactions in growth of *Tribolium castaneum*. *Can. J. of Zool.* **45**, 139—144 (1967).
13. HETZER, H. O., and W. R. HARVEY: Selection for high and low fatness in swine. *J. of Animal Sci.* **26**, 1244—1251 (1967).
14. JOHNSON, A. S., and V. S. ASMUNDSON: Genetic and environmental factors affecting size of body and body parts of turkeys. *Poultry Sci.* **36**, 1052—1057 (1957).
15. KING, S. C., and C. R. HENDERSON: Variance component analysis in heritability studies. *Poultry Sci.* **33**, 147—154 (1954).
16. MARTIN, G. A., and A. E. BELL: An experimental check on the accuracy of prediction of response during selection. In: *Biometrical Genetics*, edited by O. KEMPTHORNE, pp. 178—187. New York: Pergamon Press 1960.
17. MOLL, R. H., M. F. LINDSEY, and H. F. ROBINSON: Estimates of genetic variances and level of dominance in maize. *Genetics* **49**, 411—423 (1964).
18. RAHNEFELD, G. W., W. J. BOYLAND, R. E. COMSTOCK, and MADHO SINGH: Mass selection for post-weaning growth in mice. *Genetics* **48**, 1567—1583 (1963).
19. ROJAS, BASILIO A., and G. F. SPRAGUE: A comparison of variance components in corn yield trials III. General and specific combining ability and their interaction with location and years. *Agronomy J.* **44**, 462—466 (1952).
20. SIEGEL, P. B.: Selection for body weight at eight weeks of age. *Poultry Sci.* **41**, 954—962 (1962).

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