
UNIVERSITY OF MISSOURI-COLUMBIA
COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
ELMER R. KIEHL, DIRECTOR

Genotype x Environment Interactions in Animals

Theoretical Considerations and Review Findings

S. N. PANI AND J. F. LASLEY



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Genotype x Environment Interactions in Animals¹

Theoretical Considerations and Review of Findings²

S. N. PANI³ and J. F. LASLEY

INTRODUCTION

The phenotype of an individual animal is a function of its genotype and environment. It is the sole information available to the animal breeder for evaluating the breeding values of the animals whether measurements are made on the individuals or on their relatives. The problem of evaluation would be easy if the effects of genotype and environment on the phenotype were just additive. But, in addition to their additive effects, there may be a non-additive relationship between genotype and environment, as was recognized by Wright (1939) among others of that time.

Statistically, the additive and non-additive relationships between genotype and environment are respectively expressed as linear and non-linear and the latter is referred to as genotype-environment interaction. Thus, in statistics it is described as failure of the effects to be additive. In animal breeding, this means that the effect of an environment on two genotypes is not the same, or in other words, the effect of genotype on the phenotype is not the same in two different environments. Therefore, in the presence of interactions, the phenotypic difference between genotype A and genotype B is not the same in environment X as it is in environment Y (Lush, 1951). Sometimes it is also referred to as a differential response of the genotypes over the environments.

Variation being the basis of genetic studies, there should be at least two genotypes and two environments to recognize the importance of genotype-environment interaction (henceforth referred to as "interaction"). A simple example involving the expression of a qualitative trait such as Himalayan albinism

¹Department of Animal Husbandry.

²A part of a Ph.D. thesis submitted by S. N. Pani.

³Present address: Department of Animal Husbandry, Orissa University of Agriculture and Technology, Bhubaneswar-3, Orissa, India.

in rabbits as mentioned in almost every textbook of genetics will illustrate this point. The change in the environment

Genotype	Phenotype	
	Warm	Cold
C C	black	black
c ^h c ^h	himalayan albino	black

from warm to cold brings about a change in the expression of one genotype but has no effect on the other, although both genotypes affect the same trait. The physiological basis of this difference is well known. A similar situation is also seen with the known sex-influenced traits (as cited in any textbook of genetics) such as mahogany and red patches in Ayrshire cattle, development of horns in some breeds of sheep and baldness in man, where the phenotypic expression of the heterozygotes depends on the sex of the individual in which it is present but sex has no effect on the homozygotes. In these examples, the sex of the individual is the environment.

The effect of interaction on quantitative traits may be visualized on the same basis, although a different methodology is followed in estimating its importance, as is the case with estimation of any genetic parameter. However, the importance of interactions in animal breeding varies a great deal depending on the type of genotype and environment involved in the interaction. Genotypic differences may be between families, lines, strains, breeds, species, or sometimes even between genera. Likewise, environmental differences may be between climates (or any of its several components), management practices, nutritional regimes, types of housing, or any of the several external environmental factors; or they may be internal such as differences between age groups, sexes; or even intracellular such as cytoplasmic components like *Kappa particle* in *paramecium*, where, a nucleocytoplasmic interaction is involved in determining the phenotype.

Thus, there can be as many environmental differences as we can think of and consequently the possible combinations of genotype and environment are many. In the past, many have attempted to classify different types of interactions on as simple a basis as possible to make it meaningful. The first of these attempts was by Haldane (1946). Considering two genotypes (A,B) and two environments (X,Y) as an example, he tabulated six different types of interactions with the criterion that genotype A in environment X had always the highest rank. He has rightly pointed out that differences between all, some, or none may be statistically significant and that the ranking order of the genotypes may also be any one of the many possibilities. Thus, he has further stated that with m genotypes and n environments, there would be

$$\frac{(mn)!}{m! n!} \text{ possible types of interactions.}$$

The six types of interactions tabulated by Haldane were later shown graphically by McBride (1958) (Fig. 1). At the same time, Mather and Jones (1958) defined each of Haldane's six types in terms of the relative magnitudes of genotypic (d_a), environmental (e_1) and interaction (g_1) effects, where d_a and e_1 are the respective deviations of average values of genotypes (over both environments) and environments (over both genotypes) from the overall mean (sign ignored) and g_1 is estimated by $(AA:X + aa:Y) - (AA:Y + aa:X)$ with sign ignored. These relationships, as presented by them, are shown in Table 1.

TABLE 1. HALDANE'S SIX RELATIONS OF FOUR DIFFERENT PHENOTYPES GIVEN BY TWO GENOTYPES AND TWO ENVIRONMENTS, SHOWING THEIR DEFINITIONS BY THE RELATIVE MAGNITUDE OF d_a , e_1 and g_1 (AFTER MATHER AND JONES, 1958)

Relations	Environment	Genotype ^a		Definition
		AA	aa	
1a	X	1	3	$d_a > e_1 > g_1$
	Y	2	4	
1b	X	1	2	$e_1 > d_a > g_1$
	Y	3	4	
2	X	1	2	$e_1 > g_1 > d_a$
	Y	4	3	
3	X	1	4	$d_a > g_1 > e_1$
	Y	2	3	
4a	X	1	4	$g_1 > d_a > e_1$
	Y	3	2	
4b	X	1	3	$g_1 > e_1 > d_a$
	Y	4	2	

a The genotypes were denoted as A and B by Haldane (1946). The numbers 1, 2, 3 and 4 represent the ranking of the phenotypes in descending order.

It may be seen from the method of estimating the interaction effect that g_1 can be either positive or negative. So, later, considering the sign of g_1 , Van Der Veen (1959) tabulated Haldane's six types with conditions of $d > e$, $d = e$ and $d < e$. However, Haldane did not specify the genotypes and environments as his

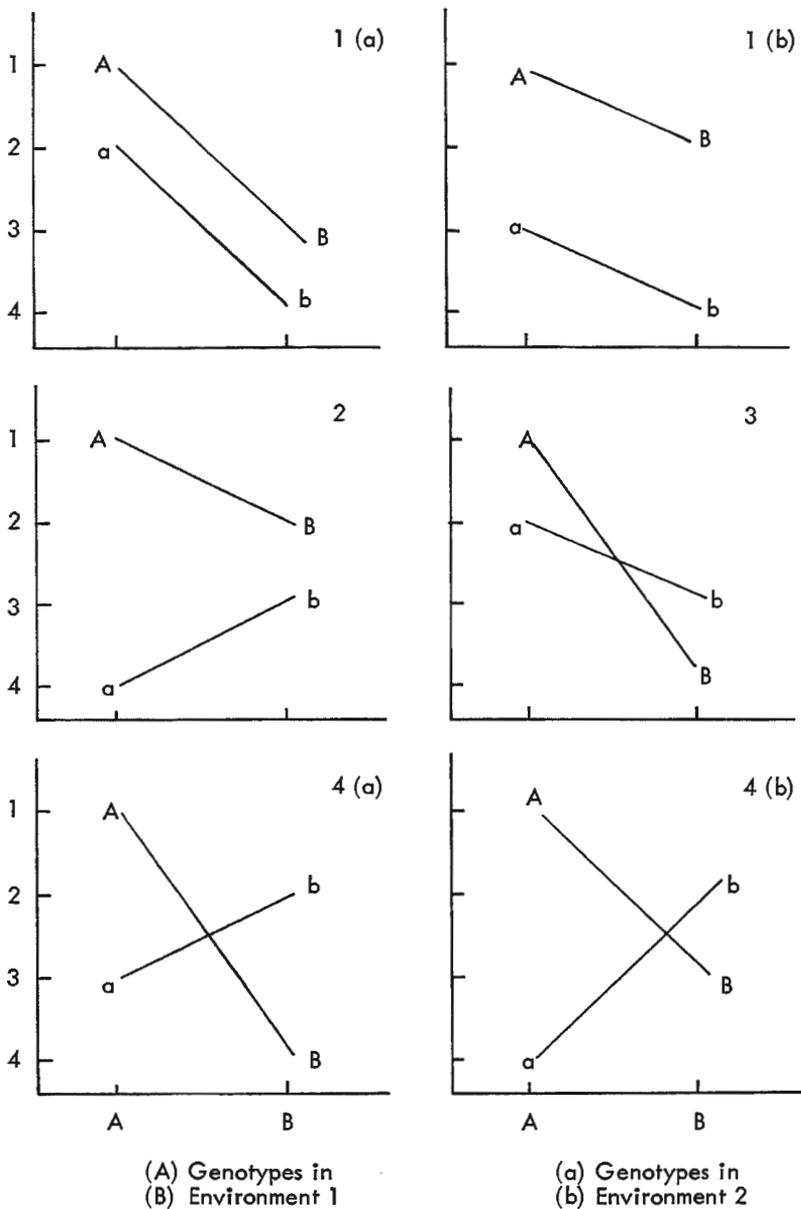


Fig. 1. Genotype Environment Interactions suggested by Haldane (1946) (After McBride, 1958).

classification was in general for any two genotypes and two environments. This has led other workers to classify interactions with some specification of the genotypes and the environments. McBride (1958) proposed to classify genotypes as "inter" and "intra" populations and environments as "macro" and "micro." His types of interaction, as presented in a tabular form are shown below (Table 2).

TABLE 2. A CLASSIFICATION OF GENOTOYPE-ENVIRONMENT INTERACTIONS
(AFTER McBRIDE, 1958)

	Microenvironments	Macroenvironments
Intra-population genotypes	Type A	Type B
Inter-population genotypes	Type C	Type D

By "macro-environments," he referred to such environmental differences as different climates and even different management practices and "micro-environments" to such environmental fluctuations as presence of subclinical infections (which may be removed by use of antibiotics) which occur even when all animals are apparently treated alike, described as "intangible" by Wright (1921). However, it may be noted that the word "population" may be any group of individuals even if the use is restricted to "Mendelian populations."

A similar attempt was made by Dunlop (1962) to classify interactions, describing the genotypes and the environments as "large" or "small." He defined small genetic differences as those occurring among individuals of a single flock or the related flocks of a breed or strain, and large genetic differences as those between strains, breeds, species, or even wider genetic divisions. Similarly, he defined small environmental differences as those occurring from individual to individual in a single general environment and large environmental differences as those between districts or regions, or widely different husbandry or nutritional regimes. His method of classification is reproduced here (Fig. 2) for illustration. It may be noted that the "macro" and "micro" environments suggested by McBride (1958) and the "large" and "small" environmental differences put forward by Dunlop (1962) are the same. However, Dunlop attempted to define the two genotypic classes with a line of demarcation along the range of genetic width among possible genotypes. All the same, it may be seen that each of his genotypic classes still included genotypes of varying genetic width.

In view of the fact that there are numerous possible combinations of genotypes and environments, probably it is impractical, if not impossible to define each of these. Thus the best way to express the type of interaction is to mention the particular genotypic and environmental differences used in an experiment, which, as a matter of fact, is the prevailing procedure. Although the classifications reported by McBride (1958) and Dunlop (1962) will continue to serve as

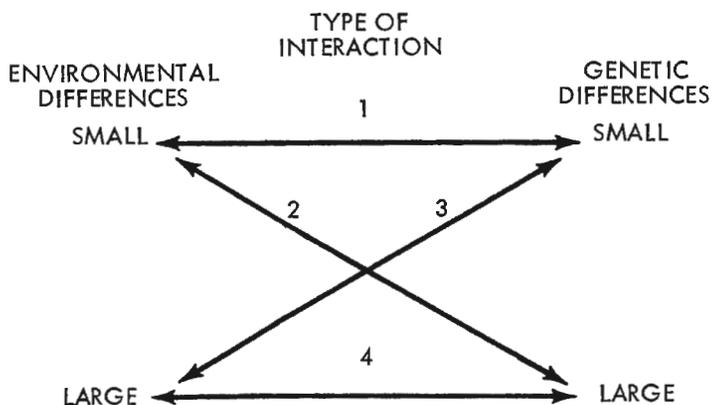


Fig. 2. Types of Heredity X Environment Interaction
(After Dunlop, 1962)

guidelines to classify interactions in a broad sense, it may be noted that no two genotypes, unless they are identical twins (restricting the discussion to mammals and birds), and no two environments to which the animals are exposed can be alike. Probably Haldane was right in not specifying the genotypes and environments, especially when his classification was to be used on the basis of the results of an experiment, a point which was probably not recognized by many who criticized him. However, he ranked individual genotype-environment combinations rather than the genotypes in different environments and did not consider statistical significance of the interaction effect for purposes of classification, although he rightly pointed out the possibilities of being statistically significant or not.

Based on Haldane's viewpoints but taking into consideration the ranking of the genotypes in different environments, statistical significance of interaction effects, and the different types of interactions reported in the literature (e.g., Van Vleck, 1963; Van Vleck *et al.*, 1963), Pani (1971) proposed a new method of classification of interactions. His classification (Types 1-4) is presented in Table 3 and Fig. 3.

In animal breeding, we are interested in knowing if the ranks of the genotypes under consideration change from one environment to the other and also if the interaction effects are statistically significant. Thus, Pani's (1971) classification was formulated mainly for practical application in breeding of animals for different environments. However, it may be pointed out that the lines in his graphical presentation may rotate within certain limits. His type 3 reflects the kind of interaction where a difference in heritability (difference in the magnitude of genetic width) but no change in the ranks is noted. In type 4, however, the

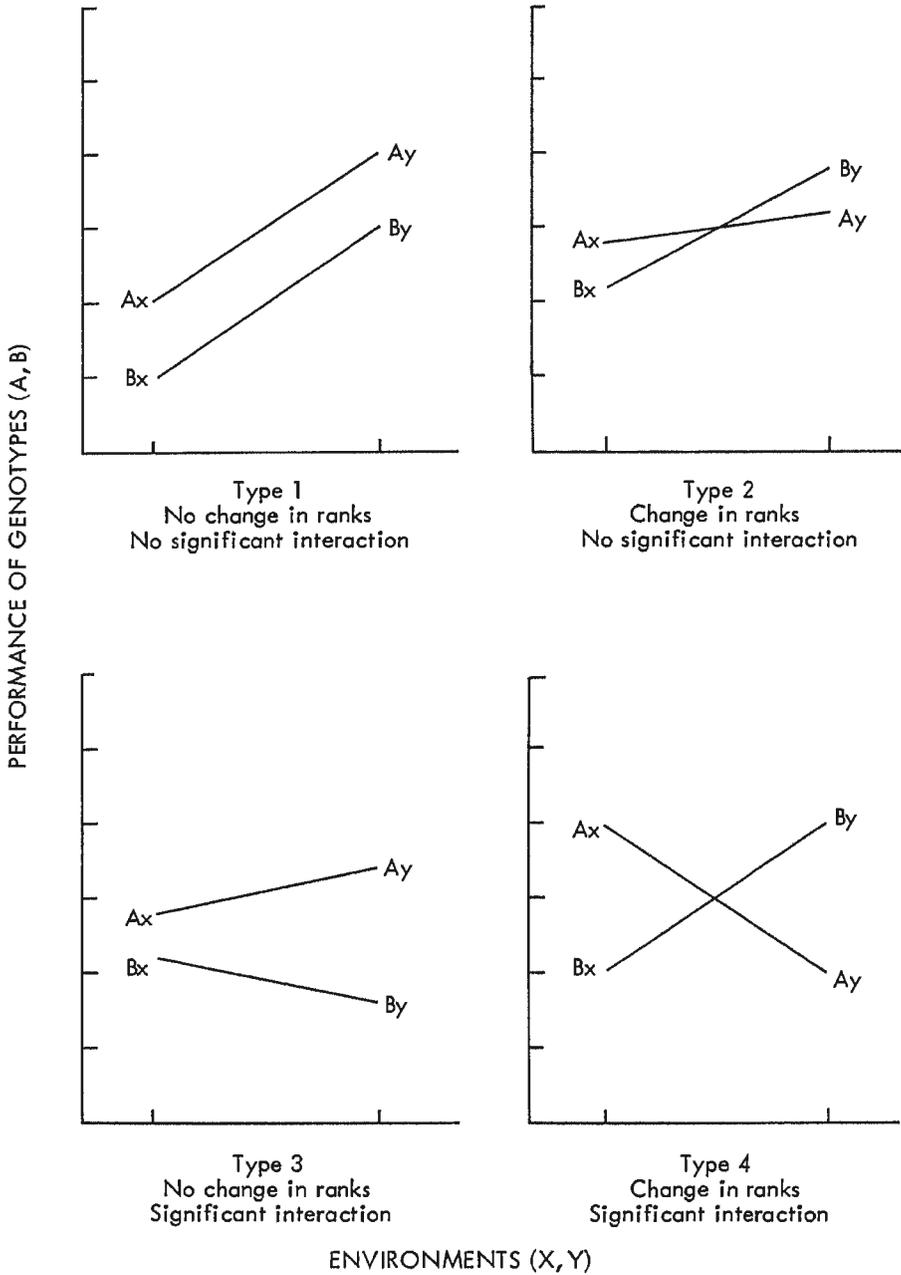


Fig. 3. A classification of genotype x environment interactions specially designed for use in farm animal studies (Pani, 1971)

TABLE 3. CLASSIFICATION OF GENOTYPE-ENVIRONMENT INTERACTIONS (PANI, 1971)

	Interactions not statistically significant	Interactions statistically significant
No change in the ranks of the genotypes	Type 1	Type 3
Change in the ranks of the genotypes	Type 2	Type 4

estimate of h^2 (being in squares) may or may not accompany the change in the ranks.

Importance of Interactions in Animal Breeding

Correct evaluation of the genotypes from their respective phenotypes is the basis of all animal breeding plans. In the presence of interaction, it will vary from one environment (whether "macro" or "micro") to another, resulting in a change of the ranking of the animals or at least in the magnitude of their differences. The effect of the former type is obvious. The latter type, however, will bring about a change in heritability and selection differential and so will affect effectiveness of selection. Various suggestions have been put forward by many eminent people in this field. For example, Wright (1939) suggested that in presence of non-additive interaction, a race has to be bred for each ecological niche large enough to support one. However, research on the importance of interaction on the effectiveness of selection was stimulated only after Hammond (1947) suggested that to make maximum improvement through selection, the animals be bred in the most favorable environment that is necessary for the fullest expression of the character and that once developed, they can also be used in other environments, provided that other characters required by the new environment are also present in the animal. One of the examples he cited was the failure of temperate dairy cattle to perform as well in the tropical areas. He believed that variability in quantitative characters would be greatest in conditions necessary for the maximum expression of the character and thus selection would be most effective. By "most favorable environment," he referred to the optimum environment required for the fullest expression of the trait. Statistically, it refers to the fullest expression of the linear effect of the environment but not the non-linear part.

Examples of such conditions may be vaccination against diseases, checking subclinical infections through use of antibiotics, and such other practices that are economically feasible. Now we all recognize that these constitute the basis of a successful livestock enterprise. However, it is not always possible to know what other characters are required in the new environment, especially if the

change requires micro physiological differences, as is seen with the appetite of the animals.

Thus, a different view was expressed by Falconer (1952) and Falconer and Latyszewski (1952), stating that the genes affecting the character in the two environments need not be the same. They added that the performance in two environments may be treated as two different traits and the problem may be treated as one of genetic correlations. The results of their experiment (to be reviewed later) on selection for growth in mice under two planes of nutrition proved their viewpoints. However, they pointed out that the only justification for selecting in a different environment would be a higher estimate of heritability.

Statements by other investigators made independently of Hammond's suggestions during the years 1947-1952 are noteworthy in emphasizing the importance of interactions:

Quoting Dobzhansky (1950), "heredity does not determine traits; it determines, according to somewhat awkward expression proposed by the Danish biologist Raunkaier, the 'norm of reaction' of the organism to the environment." He has further stated that the adaptedness of a mutant and the ancestral type may be different in different environments and the number and relative frequencies of the two would depend on the abundance of the kinds of environments. The significance of his statement in relation to selection can be easily seen, if we are dealing with micro environments such as the presence of sub-clinical infection in some animals, differences in social dominance and so on, which are not easily identifiable.

That the kind of environment in which the animals are to be kept is important in the presence of interactions, has also been emphasized by Lush (1951).

These views leave no doubt that the planning of a breeding program depends as much on the magnitude of interaction as it does on the estimated values of other genetic parameters. The necessity of estimating the importance of the interaction between heredity and environment and its application in animal breeding has been increasingly felt by livestock men who specialized in their business. Breeding stock such as domestic fowl are produced at a breeder's farm under the most favorable conditions but used in the commercial farms; because of extensive use of artificial insemination, especially in dairy cattle, sires are reared at one place but used over wide geographical areas; underdeveloped and developing countries, with a view to improving the productivity of their livestock, import animals from other countries, where the animals were selected for high productivity under different environments. These are, in brief, the general statements indicating the importance of interactions in animal breeding. Its specific effects, especially on the effectiveness of selection, will be discussed later.

Different Methods of Detecting the Presence of Interaction

A genotype-environment interaction is defined as the differential response of a genotype in different environments. All methods in estimating its impor-

tance are based on the differences in the performance of one genotype over environments as compared to other genotypes. To describe it in different words, all estimates are based on the differences of an environmental effect on different genotypes as compared to that of another environment. The description and discussion of different methods, as reported by various workers follows.

I. Ranking of Genotypes in Each Environment: Following Haldane (1946), ranking order of genotypes in each of the environments has been the most common method of getting an indication of the presence of interaction. This is really what is important for effective selection, especially in such situations as sire evaluation from progeny test results. However, as pointed out by Haldane, the interaction may or may not be statistically significant and the ranking order may or may not change in either situation. Thus, ranking of genotypes, if not accompanied by analysis of variance and a statistical test for significance of interaction, probably cannot be a precise method.

II. Differences in Response of Each of the Genotypes in two Environments: One of the simplest ways of getting an indication of the presence of interactions is to compare the differences in the performance of each of the genotypes in two environments. If these differences vary a great deal in their magnitude and from *t* tests (two groups for each genotype) the levels of significance are found to be heterogenous, the presence of significant interaction is strongly indicated. Thus it is close to the method of genetic correlation suggested by Falconer (1952) in estimating the importance of interactions. This method, as presented by Osborne (1951) on differences in sexual maturity of Brown Leghorn pullets for each of the sire families hatched at two different dates (periods) is presented in Table 4.

TABLE 4. RESULTS OF T TESTS BETWEEN MEANS OF PERIODS FOR EACH SIRE (AFTER OSBORNE, 1951)

	Sire							
	1	2	3	4	5	6	7	8
Difference of means	+10	-10	-8	+13	-1	+16	+8	-18
\pm	1.13	1.82	1.71	1.79	--	2.18	1.47	2.14
Upper limit of probability	0.3	0.1	0.1	0.1	--	0.05	0.20	0.05

However, this method, though more precise than the previous one, still gives only an indication of the presence of interaction.

III. Regression of Measurements of a Trait on Environmental Levels for Each Genotype: This is similar to the preceding method in that the effects of different environments separately for each genotype are taken into account. However, the application of the former is limited only to two environments at a time, whereas this method can be used for any number of environments. The

statistic involved in this method is to calculate the regression of the measurements of a trait on the environmental levels within each genotype and then test for heterogeneity of the regression coefficients. The following is an example of this method as reported by Osborne (1954) on age at sexual maturity of Brown Leghorn pullers over dates of hatch (Table 5).

TABLE 5. FAMILY REGRESSION COEFFICIENTS OF AGE AT SEXUAL MATURITY ON DATE OF HATCH, 1948 (AFTER OSBORNE, 1954)

Sire	1	2	3	4
	-5.23	-0.27	+0.15	+0.53
	0.31	-0.29	+0.18	+1.54
	-3.13	+1.78	+0.44	+1.35
	-1.49	-4.48	-----	+0.81
Analysis of heterogeneity			d.f.	M.S.
Sires			3	5888**
Dams within sires			12	1046
Pooled between families			15	2014**
Error			47	619

**P < .01.

IV. Orthogonal Comparison of Subclasses In a 2 x 2, (2²), factorial design with two genotypes (A,B) and two environments (X,Y), the interaction effect can be estimated by the difference between the sums of the diagonal subclasses. Diagrammatically, the subclasses are:

		Environments	
		X	Y
genotypes	A	AX	AY
	B	BX	BY

and the interaction effect is given by $[(AX + BY) - (AY + BX)]$. This was stated by Mather and Jones (1958) and King and Young (1955) expressed the interaction effects as a percentage of the overall mean to facilitate their comparison of several subcharacters of wool production. The use of this method may be easily seen from the following table (Table 6) from King and Young (1955). The method can be extended to more subclasses, for which the procedure is described in various textbooks on statistics (for example, Snedecor, 1956, Chapter

TABLE 6. MEAN VALUES FOR WOOL CHARACTERS IN THE WINTER PERIOD - MEDULLATED FIBRES EXCLUDED (AFTER KING AND YOUNG, 1955)

	Low plane of nutrition		High plane of nutrition		Inter-action	Percentage inter-action
	Blackface	Cheviot	Blackface	Cheviot		
Density (fibres/sq. cm.)	694	1407	863	1939	-181	-14.8
Length (cm.)	3.39	3.49	4.81	4.54	+0.185	+4.6
Diameter (μ)	21.4	23.8	27.4	32.3	-1.2	-4.8
Cross-sectional area (sq. μ)	391.4	491.7	619.8	859.5	-69.7	-11.8

12). However, unless accompanied by an F test for statistical significance of interaction, the estimates of interaction effects will not be meaningful.

V. Factorial Analysis of Variance: The statistical method in estimating the interaction of factors in a factorial design has been known for many years (e.g., Yates and Cochran, 1938). However, its use in animal breeding was accepted widely by quantitative geneticists only after Falconer (1952) extended the idea of genetic correlation, considering the expression of a genotype in two environments as two different traits. It is the most common method used at present in estimating the importance and testing for significance of interaction. The assumptions with regard to the distribution of the main effects would vary from one experiment to the other. Usually, however, the genotypes are assumed to be random and the environments either random or fixed depending on their nature. For example, the effects of locations (or regions) deliberately chosen, nutritional levels, methods of housing, years, sex and such others are considered fixed, whereas such effects as locations chosen at random are considered as random. The significance of this assumption can be easily seen from the formulae for calculating genetic correlations from variance components, which will be presented later. In either case the appropriate statistical model is:

$$Y_{ijk} = \mu + (A)_i + (B)_j + (AB)_{ij} + (E)_{ijk}$$

where

$i = 1, \dots, a$ environments

$j = 1, \dots, b$ genotypes

$k = 1, \dots, n$ individuals per genotype-environment subclass

Y_{ijk} is the observation on the k^{th} individual of j^{th} genotype in the i^{th} environment;

μ is the fixed underlying population mean;

$(A)_i$ is the effect of the environment i averaged over all genotypes;

$(B)_j$ is the effect of the genotype j averaged over all environments;

$(AB)_{ij}$ is the interaction of genotype j with environment i ;

and $(E)_{ijk}$ is the deviation of individual K from the mean of the j^{th} genotype - i^{th} environment subclass.

Assumptions on Distribution of the Effects

$(A)_i = N(0, \sigma_A^2)$ (*Random*) or $\Sigma(A)_i = 0$ (*Fixed*);

$(B)_j = N(0, \sigma_B^2)$ (*Random*);

$(AB)_{ij} = N(0, \sigma_{AB}^2)$ (in both *Random* and *Mixed* model) (Harvey, 1960, p. 54);

$(E)_{ijk} = N(0, \sigma_E^2)$ (uncontrolled, uncorrelated random effects that vary among individuals);

$(A)_i$, $(B)_j$, $(AB)_{ij}$ and $(E)_{ijk}$ are independent and uncorrelated;

Test of Hypothesis

$H_0 : \sigma_{ij}^2 = 0$

vs

$H_A : \sigma_{ij}^2 \neq 0$

α (probability level for statistical significance chosen *a priori*) set at .10 (for example)

Test rejects H_0 if F_{v_1, v_2} calc. $\geq F_{v_1, v_2, \alpha}$

The expectations of the mean squares for either model are shown in Table 7. If both genotypes and environments are considered fixed, the interaction effects

TABLE 7. EXPECTATIONS OF MEAN SQUARES (E.M.S.) IN A TWO-WAY FACTORIAL ANALYSIS OF VARIANCE

Source	d.f.	E.M.S. (<u>Random</u>)	E.M.S. (<u>Mixed</u>), A fixed
Environments (A)	a - 1	$\sigma_E^2 + n\sigma_{AB}^2 + nb\sigma_A^2$	$\sigma_E^2 + n\sigma_{AB}^2 + nbk_A^2$
Genotypes (B)	b - 1	$\sigma_E^2 + n\sigma_{AB}^2 + na\sigma_B^2$	$\sigma_E^2 + na\sigma_B^2$
Interaction (AB)	(a - 1) (b - 1)	$\sigma_E^2 + n\sigma_{AB}^2$	$\sigma_E^2 + n\sigma_{AB}^2$
Error	ab (n - 1)	σ_E^2	σ_E^2

are also fixed, $\Sigma(AB)_{ij} = 0$ (Harvey, 1960, p. 54). The *Fixed* and *Random* models are known respectively as *Model I* and *Model II* of Eisenhart (1947). The analysis of variance is followed by the usual procedure of equating the E.M.S. with the respective observed mean squares to estimate the components of variance. The total variance per observation would then be σ_T^2 , which is " $\sigma_A^2 + \sigma_B^2 + \sigma_{AB}^2 + \sigma_E^2$ " in a *Random* model and " $\sigma_B^2 + \sigma_{AB}^2 + \sigma_E^2$ " in a *Mixed* model (A being fixed). Following the estimation of each of those variance components, there

are several ways of evaluating the importance of interactions in animal breeding plans.

On the basis of Falconer's (1952) idea, Robertson (1959) presented formulae with their appropriate variances for estimating the genetic correlation of the performance of the same genotypes in two or more environments. They are:

(a) with two environments:

$$r_g = \frac{A - B}{A + B - 2C}$$

and (b) with more than two (p) environments:

$$r_g = \frac{A - B}{A - C + (p - 1)(B - C)}$$

where, A, B and C are the respective mean squares for genotypes (groups), group x environment interaction and error (remainder). The respective variances are:

$$(a) V(r_g) = \frac{[nt(1 - r_g^2) + (1 - t)]^2 + r_g^2(1 - t)^2}{(N - 1)n^2t^2} + \frac{r_g^2(1 - t)^2}{N(n - 1)n^2t^2}$$

However, when t is small and n is large, it simplifies to:

$$V(r_g) \approx \frac{[1 + nt(1 - r_g^2)]^2 + r_g^2}{(N - 1)n^2t^2} \quad (\text{with two environments});$$

and

$$(b) V(r_g) = \frac{2\{[1 - t + nt(1 - r_g)] [1 + (p - 1)r_g]^2 + (p - 1)r_g^2(1 - t)^2\}}{(N - 1)p(p - 1)n^2t^2} + \frac{2r_g^2(1 - t)^2}{Npn^2(n - 1)t^2} \quad (\text{with } p \text{ environments}).$$

where

N is the number of groups of genotypes;

n is the number of relatives in each group-environment subclass;

t is the intraclass correlation assumed to be the same in all the environments;

and r_g is the genetic correlation.

He has also provided the composition of the component of variance for interaction. With two environments:

$$\sigma_{GE}^2 = \frac{1}{2}(\sigma_{G1} - \sigma_{G2})^2 + \sigma_{G1}\sigma_{G2}(1 - r_g)$$

Here σ_{G1} and σ_{G2} refer to the genetic standard deviations in environment 1 and 2, respectively, and r_g is the genetic correlation between the performance of genotypes in the two environments. It may be noted that with equal heritabilities in both the environments, $\sigma_{G1} = \sigma_{G2}$ and the first quantity in the expression becomes zero. Also with $r_g = 1$, the second part becomes zero. Thus the interaction component is greater than zero only when $\sigma_{G1} \neq \sigma_{G2}$ and/or $r_g < 1$. With more than two environments the mean value of the first quantity $\frac{1}{2}(\sigma_{G1} - \sigma_{G2})^2$ is simply the variance of the genetic scales, or $V(\sigma_{G1})$ and interaction component $\sigma_{GE}^2 = V(\sigma_{G1}) + \sigma_{G1}\sigma_{Gj}(1 - r_g)$ (Dickerson, 1962).

As stated by Robertson (1959), the estimate of the genetic correlation between performance in two or more environments as a quantitative expression of genotype-environment interaction is of value in giving a measure of the practical, rather than the statistical, significance of the results. He suggested that an estimate of r_g around 0.8 would be of biological or agricultural importance and no experiment on interaction between genotype and environment would be considered worth doing unless a genetic correlation of 0.6 significant difference from unity is detected.

A similar method for estimating a genetic correlation from genetic and genotype by environment interaction components of variance (σ^2_G , σ^2_{GE}) was presented by Dickerson (1962), which is expressed by

$$r_g = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE}}$$

This formula was derived under the assumption of the same genetic variance in each of the environments. Any inequality of genetic variance would bias σ^2_{GE} upwards and so, when corrected for this bias,

$$\sigma^2_{GE1} = \sigma^2_{GE} - V(\sigma_G)$$

and

$$r_g^1 = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE} - V(\sigma_G)}$$

(Dickerson, 1962). In case of two environments, the appropriate quantity $\frac{1}{2}(\sigma_{G1} - \sigma_{G2})^2$ is to be removed from σ^2_{GE} , when $\sigma_{G1} \neq \sigma_{G2}$. It may be noted from the formula why a perfect correlation

$$(r_g^1 = 1.00)$$

means no interaction of genotype by environment.

It has been stated that the composition of mean squares in any analysis of variance depends on the statistical model, whether *random*, *mixed*, or *fixed*, which is essential in equating the expectations with observed mean squares for estimating the variance components. Since Robertson (1959) gave his formulae in terms of mean squares, the nature of the statistical model will not influence the estimate. However, Dickerson's (1962) formula being in terms of variance components, the nature of the statistical model is important in estimating the variance components and, consequently, the estimate of r_g . As the nature of the statistical model was not discussed in either of the papers cited above, Yamada (1962) presented formulae for both *random* and *mixed* models to estimate genetic correlations between performance in two or more environments. They are:

$$(a) r_g = \frac{\sigma^2_b}{\sigma^2_b + \sigma^2_I - V(\sigma_b)} \quad (\text{For } \textit{Random} \text{ model; two or more environments; same as the one by Dickerson, 1962})$$

$$(b) r_g = \frac{\sigma^2_b - \frac{1}{2}\sigma^2_I}{\sigma^2_b + \frac{1}{2}\sigma^2_I - \frac{1}{2}(\sigma_{b1} - \sigma_{b2})^2} \quad (\text{For } \textit{Mixed} \text{ model; two environments})$$

$$\text{and (c) } r_g = \frac{\sigma_b^2 - \frac{1}{K} \sigma_I^2}{\sigma_b^2 + \frac{K-1}{K} \sigma_I^2 - V(\sigma_b)} \quad (\text{For } \textit{Mixed} \text{ model; } K \text{ environments})$$

In each of Yamada's three equations, σ_b^2 and σ_I^2 are the between-group and interaction-variance components, respectively, and used θ (σ_b) in *mixed* model in place of $V(\sigma_b)$ as presented here. These formulae can be verified by substituting the appropriate expectations in the mean squares of Robertson's formulae. Obviously, Dickerson's formula was for a *random* model. However, there is a difference in the nature of the two formulae. The one for a *random* model will always estimate a value of r_g anywhere from zero to unity; whereas, with the formula for a *mixed* model, there is a possibility of getting negative estimates if the interaction component is extremely large as compared to the genetic component, or when the genetic component is zero in the presence of interaction.

The variance component estimates derived from a two-way analysis can be used in several other ways in presenting the importance of genotype by environment interaction. With the notations used earlier in the analysis of variance (Table 1), these other ways are:

(i) $\frac{\sigma_{AB}^2}{\sigma_T^2}$ in % of σ_T^2 : If each of the variance components is expressed as % of σ_T^2 , their relative magnitudes and so the importance of σ_{AB}^2 can easily be seen.

(ii) $\frac{\sigma_{AB}^2}{\sigma_B^2 + \sigma_{AB}^2}$: It is the proportion of the interaction variance from the total genetic variance. This quantity has been expressed as "genetic bias" by Beck and Baker (1964). It is interesting to note that in a *random* model, the genetic correlation (r_g) and the "genetic bias" present the importance of interactions in exactly opposite ways. The larger the estimate of r_g , the less important is the interaction; whereas, the larger the "genetic bias," the greater its importance. Further, both add to unity

$$\left(\frac{\sigma_B^2}{\sigma_B^2 + \sigma_{AB}^2} + \frac{\sigma_{AB}^2}{\sigma_B^2 + \sigma_{AB}^2} = 1.00 \right).$$

(iii) *Repeatability estimates*: These are usually the estimates of intraclass correlation coefficients. As mentioned in Table 7, suppose we have b genotypes tested over a environments. By definition, an intraclass correlation coefficient is the proportion of between-group variance to the total variance per observation. The latter, however, depends upon the practical application of the results. If, for example, the interest is to use the average performance of a genotype in one environment as an estimate of its breeding value but used in a different environ-

ment such as years, sexes, etc., the individual observations would be the mean values of the genotypes in each environment with a variance of

$$\sigma^2_A + \sigma^2_B + \sigma^2_{AB} + \frac{\sigma^2_E}{n} \text{ (for } \textit{Random} \text{ model) or}$$

$$\sigma^2_B + \sigma^2_{AB} + \frac{\sigma^2_E}{n} \text{ (for } \textit{Mixed} \text{ model, A fixed) (n as defined in Table 7).}$$

Then the repeatability estimates are:

$$(a) r = \frac{\sigma^2_B}{\sigma^2_A + \sigma^2_B + \sigma^2_{AB} + \frac{\sigma^2_E}{n}} \text{ (for a } \textit{random} \text{ model)}$$

$$\text{and (b) } r = \frac{\sigma^2_B}{\sigma^2_B + \sigma^2_{AB} + \frac{\sigma^2_E}{n}} \text{ (for a } \textit{mixed} \text{ model)}$$

However, if the average performance of a genotype over all the environments is used as its general performance ability, a situation which is encountered, for example, in random sample tests in poultry or evaluation of dairy sires from their performance in different herds, the variance of such a value would be

$$\frac{\sigma^2_A}{a} + \sigma^2_B + \frac{\sigma^2_{AB}}{a} + \frac{\sigma^2_E}{an} \text{ (for a } \textit{random} \text{ model) and}$$

$$\sigma^2_B + \frac{\sigma^2_{AB}}{a} + \frac{\sigma^2_E}{an} \text{ (for a } \textit{mixed} \text{ model).}$$

The repeatability estimates in these cases would then be:

$$(a) r = \frac{\sigma^2_B}{\frac{\sigma^2_A}{a} + \sigma^2_B + \frac{\sigma^2_{AB}}{a} + \frac{\sigma^2_E}{an}} \text{ (for a } \textit{Random} \text{ model)}$$

$$\text{and (b) } r = \frac{\sigma^2_B}{\sigma^2_B + \frac{\sigma^2_{AB}}{a} + \frac{\sigma^2_E}{an}} \text{ (for a } \textit{Mixed} \text{ model).}$$

For details of repeatability estimates, reference may be made to Nordskog and Kempthorne (1960); and Dickerson (1961). It is worth mentioning that the estimate may vary from zero to unity, a perfect repeatability meaning $r = 1.00$. It may be large or small, depending on the magnitude of the interaction component, number of environments used, and the size of n .

(iv) $\frac{\sigma^2_{AB}}{\sigma^2_B}$: This is a comparison of the relative magnitude of the two parts of the total genetic variance, *viz.*, the interaction and the genetic components. Obviously, if the ratio is large, the performance of a genotype would be less repeatable over all the environments and *vice versa*. As an example of its use, the paper by Dunlop and Young (1966) may be reviewed.

In all the methods above, the variances were estimated from a two-way factorial analysis of variance. However, as stated by Yamada (1962), one of the

most popular designs in animal breeding is the hierarchical factorial design, where each sire (S) is mated to several dams (D) and the performance of progenies from each dam is measured in two or more environments (A). The linear statistical model and the appropriate expectations of mean squares for a *mixed* model with two environments are presented here for illustration.

$$Y_{ijkl} = \mu + (A)_i + (S)_j + (AS)_{ij} + (D:S)_{jk} + A(D:S)_{ijk} + (E)_{ijkl}$$

$i = 1, 2$ environments;

$j = 1, \dots, s$ sires;

$k = 1, \dots, d$ dams within each sire;

$l = 1, \dots, n$ progeny in the i^{th} environment within k^{th} dam within j^{th} sire;

μ is the fixed underlying population mean;

A_i is the effect of i^{th} environment averaged over all progeny: dam: sire subclasses;

S_j is the effect of j^{th} sire averaged over all environments;

$(AS)_{ij}$ is the interaction of environment i and sire j ;

$(D:S)_{jk}$ is the effect of k^{th} dam: j^{th} sire;

$A(D:S)_{ijk}$ is the interaction of environment i with dam k : sire j ;

and E_{ijkl} is the deviation of the individual l from the mean of the environment i - dam k : sire j subclass.

Assumptions on Distribution of the Effects:

$$\Sigma(A)_i = 0 \text{ (fixed);}$$

$$(S)_j = N(0, \sigma^2_S) \text{ (random);}$$

$$(AS)_{ij} = N(0, \sigma^2_{AS}) \text{ (random);}$$

$$(D:S)_{jk} = N(0, \sigma^2_{D:S}) \text{ (random);}$$

$$A(D:S)_{ijk} = N(0, \sigma^2_{A(D:S)}) \text{ (random);}$$

$(E)_{ijkl} = N(0, \sigma^2_E)$ (uncontrolled, uncorrelated random effects that vary among individuals);

$(A)_i, (S)_j, (AS)_{ij}, (D:S)_{jk}, A(D:S)_{ijk}$ and $(E)_{ijkl}$ are independent and uncorrelated.

The design of the experiment may be best visualized from the following table, which is required to summarize the data.

	Environment 1	Environment 2
Sire 1	D_1 n progeny	n progeny
	.	
	.	
	.	
	D_d	
	.	
	.	
	.	
Sire s		

The analysis of variance for the *mixed* model is given in Table 8.

TABLE 8. ANALYSIS OF VARIANCE IN A NESTED FACTORIAL DESIGN

Sources	d.f.	E.M.S. (Mixed)
Environments (A)	1	$\sigma_E^2 + n\sigma_{A(D:S)}^2 + nd\sigma_{AS}^2 + sdnk_A^2$
Sires (S)	s - 1	$\sigma_E^2 + 2n\sigma_{D:S}^2 + 2nd\sigma_S^2$
Dams within sires (D:S)	s(d - 1)	$\sigma_E^2 + 2n\sigma_{D:S}^2$
A x S	s - 1	$\sigma_E^2 + n\sigma_{A(D:S)}^2 + nd\sigma_{AS}^2$
A x (D:S)	s(d - 1)	$\sigma_E^2 + n\sigma_{A(D:S)}^2$
Error	2sd(n - 1)	σ_E^2

The appropriate formulae to calculate the genetic correlation between the performances in two environments have also been given by Yamada (1962). With notations used in Table 8, they are:

$$(a) r_{gs} = \frac{\sigma_S^2 - \frac{1}{2}\sigma_{SA}^2}{\sigma_S^2 + \frac{1}{2}\sigma_{SA}^2 - \frac{1}{2}(\sigma_{S1} - \sigma_{S2})^2}$$

$$\text{and (b) } r_{gD} = \frac{\sigma_{D:S}^2 - \frac{1}{2}\sigma_{A(D:S)}^2}{\sigma_{D:S}^2 + \frac{1}{2}\sigma_{A(D:S)}^2 - \frac{1}{2}(\sigma_{D1:S} - \sigma_{D2:S})^2}$$

The subscripts 1 and 2 refer to the two environments.

Diallel or polyallel crosses are among other experimental designs sometimes used in animal breeding for estimating the genetic parameters. If these experiments are replicated over different environments (for example, locations or years), estimation of interaction effects is possible. These experiments are useful especially in estimation of the stability (repeatability) of nonadditive gene action over environments. For statistical analysis and other details, reference is made to Allard (1956), Griffing (1956) and Matzinger, and Kempthorne (1956).

An interesting relationship between the genetic correlation and the interaction variance has been presented by Yamada (1962). With his notations, σ^2_w , σ^2_I , and σ^2_b representing variance components for error, interaction, and between-group, respectively, in the two-way analysis, he has shown that with two environments, $\sigma^2_I = \frac{1}{2}(\sigma^2_{b_1} + \sigma^2_{b_2}) - \sigma_{b_{12}}$ in both the *random* and *mixed* model. With this reasoning he illustrated the relationship between the genetic correlation and interaction variance in the form of a scalene triangle, in which $r_g = \cos \theta$ based on the law of cosine. His diagram is reproduced here for illustration (Fig. 4).

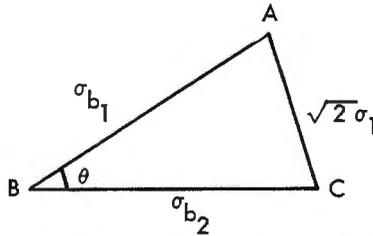


Fig. 4. Relationship between the Genetic Correlation and Interaction Variance, where $\overline{AB} = \sigma b_1$, $\overline{AC} = \sqrt{2} \sigma_I$, $\overline{BC} = \sigma b_2$, and $\cos \theta = r_g$. If $1 > r_g > 0$, we have $90^\circ > \theta > 0$; if $0 > r_g > -1$, we have $180^\circ > \theta > 90^\circ$; and if $r_g = 0$, we have $\theta = 90^\circ$ (After Yamada, 1962)

VI. Variance and Covariance Analysis: With only two environments, the genetic correlation (r_g) may be estimated from the variance and covariance components following the idea of Falconer (1952). It is given by

$$r_g = \frac{\sigma_{G_{12}}}{\sigma_{G_1} \sigma_{G_2}}$$

where $\sigma_{G_{12}}$ is the genetic covariance between the same trait measured in the two environments and σ_{G_1} and σ_{G_2} are the respective genetic standard deviations in the environments 1 and 2, respectively. The method described by Van Vleck (1963) in evaluating sires from daughter records in different herd levels is given here as an example. The method is to calculate the correlation coefficient using

the means of the daughters of each sire in the two environments. However, since each of the mean values also contains an error term,

$$\frac{\sigma^2_w}{n}$$

each of the sire components in the denominator of the formula has to be reduced by the appropriate amount of within-sire variance. This quantity of within-sire variance is estimated by

$$\frac{1}{s} \sum_i \frac{1}{n_{ij}} \sigma^2_{ej},$$

where s is the number of sires having daughters in both levels, n_{ij} is the number of daughters for the i^{th} sire in the j^{th} level and σ^2_{ej} is the within-sire variance for the j^{th} level. However, the two sire components of the denominator can also be estimated separately in their respective environments from one-way analysis of the data as reported by Wiggans and Van Vleck (1970).

This method is suggested when there are only two environments. With more than two environments, Dickerson's (1962) formula using only variance components is preferred as it would be easier than estimating r_g by the covariance method considering all combinations of two environments at a time.

Vii. Selection in two Environments: The genetic correlation can also be estimated from direct and correlated responses. If a strain is selected in environment 1, the genetic advance in that environment is known as the "direct response" (Δ^1G_1). However, if the strain is selected in another environment 2 and switched to environment 1, the genetic advance of such a strain is called the "correlated response" (Δ^1G_1) in environment 1. As stated by Falconer (1952), the ratio of the correlated response to the direct response is

$$\frac{\Delta^1G_1}{\Delta G_1} = \frac{h_2}{h_1} r_g,$$

where h_2 and h_1 are square roots of the heritability estimates in environments 1 and 2, respectively, and r_g is the genetic correlation of the performance in the two environments. On rewriting the equation, it becomes

$$r_g = \frac{\Delta^1G_1 h_1}{\Delta G_1 h_2}.$$

However, it may be noted that an assumption of equal intensity of selection in both the environments was made in deriving the equation. For further details on the estimation of the genetic correlation from experiments on selection in two environments, reference to James (1961) is suggested.

It may be noted that in the presence of significant interactions, the performance of a population (genotypes) selected in one environment will decrease if shifted to another environment, a regression that is described as "genetic slip-page" by Dickerson (1961).

Viii. Differences in the Magnitude of Heritability Estimates: As stated earlier, in the presence of an interaction there may be a change in the relative

magnitude of genotypic values in two different environments without affecting their ranking order. Thus, a significant difference in the heritability of a character in the two environments would indicate the presence of an interaction as pointed out by Van Vleck (1963) and Van Vleck *et al.* (1963). In such a situation it would be profitable to select animals in the environment where heritability is highest and use them in the other environments because the correlated response would be greater than the direct response. This may be verified from the equation for the ratio

$$\frac{\Delta^1 G_1}{\Delta G_1}$$

given earlier. Production of breeding stock of poultry at one location with a higher level of management for use in the commercial flocks at other locations; and evaluation of dairy bulls in one herd, where the level of production may be different from that in another herd in which they will be used, are examples where an application of this method may arise. Another advantage in the use of this method as stated by Van Vleck (1963) is that with higher heritability in one environment fewer progeny are required to evaluate a sire with a fixed degree of accuracy than in other environments with lower heritabilities. At this time it is appropriate to point out Falconer's (1952) conclusion that the only justification of selecting animals in an environment other than the one in which they are to live is the expectation of a great increase in the heritability estimate.

IX. Experiments with Identical Twins: In experiments with identical twins, one member of each twin pair is allotted to one of two treatments. From a two-way analysis it becomes possible to estimate variances due to heredity (between pairs), environment, and the remainder, which includes both interaction and error terms because of only one observation per subclass. So the error term is estimated separately by treating both members of some twin pairs alike and deducting from the remainder variance (as stated above); an estimate of the interaction component is thus obtained. As an example of such studies, see Bonnier and Hansson (1948).

Some Specific Effects of Interaction: The effects of interactions on the ranking of genotypes and correlated response were pointed out under the respective methods for estimating importance of a response. However, its effects, especially on the estimation of heritability, need to be presented in some detail. One of the basic requirements in estimating heritability is that the data be corrected for the known environmental effects, which otherwise would inflate the error term and the estimate of heritability would be biased downwards. This is also true for the presence of interaction effects.

Particularly in farm animals, where the number of animals per generation is small, it becomes necessary to use records of several years, including several seasons and so on, to estimate heritability coefficients. The estimates of genetic parameters so obtained are used in planning the future breeding program. So it

is necessary that the data be corrected for all such effects before the analysis is made. But all the known methods of correlation for environmental factors are based only on their average effects and there is no way of making a prior correction of data for the interaction effects. Therefore, it is suggested that with a prior knowledge of the significance of an interaction of the genotypes with the known environmental effects, the data may be classified either 2-way, 3-way or 4-way, depending on the number of environments for statistical analysis. The appropriate quantities of interaction components may then be deducted from the total variance to get unbiased estimates of heritability.

The effect of interaction on sexual dimorphism in animals has received some attention in the past. In farm animals the intensity of selection is always more in males than it is females. For characters such as growth rate, males are always faster growing than females. If there is any independence of the genetic effects on the growth rate of the two sexes or, in other words, if there is any genotype x sex interaction, the difference in the intensity of selection will accentuate the sexual dimorphism in growth in that species (Horton and McBride, 1954). The formulae for estimating the heritability of the difference between males and females and its relationship to genotype x sex interaction have been presented by Eisen and Legates (1966). They are:

$$(a) h^2_{(1-2)} = \frac{2\sigma^2_{GS}}{\sigma^2_{p(1-2)}}$$

where $h^2_{(1-2)}$ is the heritability of the difference between males and females; σ^2_{GS} is the corrected interaction component of variance $\sigma^2_{GS} - \frac{1}{2}(\sigma_{G1} - \sigma_{G2})^2$; and $\sigma^2_{p(1-2)}$ is the corrected phenotypic variance of the differences $\sigma^2_{p(1-2)} - (\sigma_{p1} - \sigma_{p2})^2$. In terms of causal components:

$$(b) h^2_{(1-2)} = \frac{4\sigma^2_{s(1-2)}}{\sigma^2_{s(1-2)} + \sigma^2_{d(1-2)} + \sigma^2_{w(1-2)}}$$

where the subscripts s, d, and w refer to sire, dam, and within progeny, respectively. Formula (a) reveals that the heritability estimate is directly proportional to the size of the interaction component. The presence of genotype x sex interactions poses another important problem in animal breeding. Early evaluation of sires for growth rate necessitates the use of data on male progeny only. Even if data on either sex are used, their numbers may be different and their proportion may vary greatly from one sire to another. Any method of correction will adjust the data only for their average effects but not for the interaction. Thus, in the presence of a large and significant interaction, it would be necessary to include progeny from both sexes. But in large animals such as cattle, it may not be practicable to obtain enough progeny from either sex within a reasonable period. The solution to this problem is not easy. Further research and thought are needed to find a solution.

To this point, the concept of genotype by environment interaction, the different classifications, the genotype's importance in animal breeding plans, and the different methods of genotype estimation have been discussed. Now it is appropriate to review the findings on the importance of interactions in various species of farm and laboratory animals.

RESULTS WITH VARIOUS SPECIES

Beef Cattle

In general, interactions are likely to be more important in farm animals than in laboratory animals as the environmental conditions for the latter are better controlled. Among farm animals, the prevailing farming practices do not permit as rigid a control of the environmental effects in raising beef cattle as is possible with dairy cattle or poultry. Thus, interaction effects are expected to be more important in beef cattle than with other farm animals, especially with the intra-population x micro-environment type. A review of the reports on different characters of economic importance in beef cattle follows:

Birth Weight.—The only environmental effects at birth would be maternal influence and sex of the calf. Other environmental factors to which the dam was exposed, if they have any effect, would be included under maternal influence. Thus, interaction effects at birth would be either genotype x sex or genotype x any other environmental factor acting through its effects on the dam. Few reports on interaction effects have been made on birth weight. From data on the male calves of 11 Hereford bulls at two locations, Woodward and Clark (1950) found no significant sire x station interaction; whereas a significant sire x region interaction was observed by Edwards *et al.* (1966).

A significant breed x year effect was found by Ellis *et al.* (1965) in a comparison of Hereford and Brahman calves. Line of sire x year and line of dam x year effects were not important in the study of Brinks *et al.* (1967), involving lines of Hereford cattle. Presence of breed x year interactions involving different breeds was also indicated by Turner and McDonald (1969). These reports indicate that the larger the genetic width between the groups and the larger the environmental differences, the more likely the presence of interactions.

Interactions involving the sex of the calf appear to be really important. Brinks *et al.* (1963) observed a differential sex response to inbreeding of calf and dam, with the former having a more pronounced effect on females and the latter a greater effect on males. Heritability estimates by the paternal half-sib method were found to be 0.32 and 0.14 in male and female calves, respectively, by Pahnish *et al.* (1964). Both of these studies were with Hereford cattle. Added to these evidences, Ellis *et al.* (1965) observed a significant breed x sex interaction, the two groups being Hereford and Brahman calves. However, sire x sex and line of dam x sex interactions were not found to be important by Bradley *et al.*

(1966). Although the reports are few, the presence of genotype x sex interactions in birth weight of calves appear to be conclusive.

Average Daily Gain (A.D.G.) (Birth to Weaning)—Environmental effects on A.D.G. include maternal effects such as milk production and mothering care of the dam in addition to the environmental influence under investigation and so the results are to be interpreted from this viewpoint. No significant sire x station interaction was observed by Woodward and Clark (1950), whereas such an interaction was found to be an important source of variation by Cunningham and Henderson (1965).

Considering years as environments, Brinks *et al.* (1967) observed no significant interactions with line of sire or line of dam, whereas important breed of sire x year effects were indicated in the study of Turner and McDonald (1969).

Studies on interactions involving sex of the calf appear to be more predominant than any other type. None of the studies from the analysis of variance of data indicated significant sire x sex interactions (Bradley *et al.*, 1966; Wilson *et al.*, 1969; Tanner *et al.*, 1969; Thrift *et al.*, 1970). However, the heritability of A.D.G. was found to be 0.01 and 0.25 for male and female calves, respectively, by Pahnish *et al.* (1964) and a differential response of sex to inbreeding of calf and dam was observed by Brinks *et al.* (1963). From these studies one may expect differences in the relative magnitude of the genotypes in the sexes without altering their ranking order for A.D.G. It may be noted that sex includes bull calves, steers, and female calves, and comparisons may be made between any two or all three.

Weaning Weight—Considerable variation exists among different regions in the age to which the weaning weights are adjusted, although usually it is around 200 days of age. Further, since weaning weight includes both birth weight and A.D.G., environmental factors affecting both these traits are likely to influence weaning weight.

In the study of Harwin *et al.* (1966), mating systems (inbred or line-cross Hereford calves) x year interactions were not important. However, line of sire x year but not line of dam x year effects were found to be significant by Brinks *et al.* (1967) and Urick *et al.* (1968). Added to these, there was an indication of important breed of sire x year interaction in the study of Turner and McDonald (1969). Differential effects of month of birth in Hereford and Angus were observed by Marlowe (1962) but breed x month of calving (or season) was found to be small both by Cundiff *et al.* (1966) and Sellers *et al.* (1969). In both the latter reports, a breed x age of dam interaction was also observed to be unimportant.

Heritability estimates from two grade Hereford herds on different nutritional levels were not found to be significantly different by Rollins and Wagnon (1956). However, breed x management (creep- and non-creep feeding) effect was found to be a significant source of variation by Sellers *et al.* (1969).

There have been more reports on interactions involving sex of the calf than any other type. These interactions do not appear to be important sources of variation from weaning weight (Knapp and Phillips, 1942; Koger and Knox, 1945; Pahnish *et al.*, 1961; Bradley *et al.*, 1966; Tanner *et al.*, 1969; Sellers *et al.*, 1969; Thrift *et al.*, 1970). However, Harwin *et al.* (1966) observed a significant sex x mating system interaction and the important sire x sex effect found by Wilson *et al.* (1969) confirmed the differential response of sex to heterosis effects reported by Stonaker (1963). Estimates of heritability indicate larger additive genetic variance in females than in males as shown in the following table.

Male	Female	Method of estimation	Author(s)
0.08 (steers)	0.69	Paternal half-sib	Carter and Kincaid, 1959
0.28 (bull calves)	0.57	Paternal half-sib	Pahnish <i>et al.</i> , 1961
0.05 (bull calves)	0.23	Paternal half-sib	Pahnish <i>et al.</i> , 1964

Although the difference was not significant in some of the reports, the trend has been consistent. It is contrary to expectation as the male sex is more favorable for growth than female sex, especially at a younger age. It would be interesting to see if the trend for heritability estimates of weight at a younger age (for example 100 days) would be different. Added to these findings, a differential response of sex to inbreeding of calf and dam was reported by Brinks *et al.* (1963).

From all of these reports, it may be seen that the importance of interactions for weaning weight varies a great deal from one instance to another. Further studies might aid in arriving at a conclusion on the importance of different types of interactions.

Weaning Score.—Brinks *et al.* (1967) observed no significant line of sire x year or line of dam x year effects but there was an indication of breed x year interactions in the study of Turner and McDonald (1969).

Knapp and Phillips (1942) found that sire x sex effects constitute an important source of variation. Heritability of weaning grade was higher in heifer calves (0.24) than in bull calves (0.08) (Pahnish *et al.*, 1964). The differential response of sex to the inbreeding of the calf and dam, as reported by Brinks *et al.* (1963), add to the importance of interactions with sex of the calf.

From these reports, interactions involving sex appear to be important sources of variation for weaning score.

Postweaning Gain.—The later the age at which the measurements are made, the larger would be the environmental effects and more likely the presence of

interactions. The different environments to which beef cattle are exposed after weaning are many as compared to the conditions prior to weaning. Thus, it is likely that the results on postweaning traits would be more variable as compared to results on preweaning traits.

Sire x location effects were not found significant by Averdunk *et al.* (1968) and Ahlschwede *et al.* (1969). However, such a source of variation was seen to be important in the study of Woodward and Clark (1950). It may be noted that the environmental conditions in locations vary greatly from one report to the other.

Interactions involving differences in nutritional level have received much attention. Results vary greatly. In some studies (Brown and Gacula, 1962; Harling *et al.*, 1963; Rollins *et al.*, 1964; Maltos and De Alba, 1967; Ahlschwede *et al.*, 1969) they were insignificant, whereas in others (Maltos *et al.*, 1961; Bond *et al.*, 1965; Bojarskii and Kadievskaja, 1966; Wiltbank *et al.*, 1969) they were important sources of variation. It may be pointed out that the genotypes and the rations used in these studies were not the same. The use of monozygotic twins by Warwick *et al.* (1964) is worth pointing out separately. With two levels of nutrition, viz., high and low, they observed a significant ration x pair interaction. Added to this, heritability estimates from two herds managed at two different levels of nutrition were .25 and -.04 as reported by Rollins and Wagon (1958) and 0.27 and 0.03 by Wagon and Rollins (1959). In view of the varying results, it would be desirable to determine the importance of genotype x nutritional level interactions, using the genotypes and rations likely to be used in a particular farm or area.

An interesting experiment was conducted by Gravir (1961), who tested the performance of two lowland and two mountain breeds at both altitudes. As the lowland breeds grew faster at both the altitudes, one would expect important breed x altitude interactions. On further analysis, Skjervold and Gravir (1961) found no evidence in support of such an assumption.

A noticeable breed x year effect was observed by Ahmad (1966) in comparing Angus and Hereford steers. Patterson *et al.* (1955), however, found no significant sire x year interaction in feedlot gains. In the study of Urick *et al.* (1968), line of sire x year interaction was found important for gain from weaning to 12 months but not in the gain from weaning to 18 months of age; the line of dam x year effect, however, was not significant for either of the gains.

Significant sire x sex interactions on postweaning gain were reported by Knapp and Phillips (1942); and Suess *et al.*, 1966. Brannang (1967) observed a differential response of two breeds (Swedish Friesians and Swedish Red-and-Whites) to castration effects, the reduction in growth rate in steers being greatest for progeny groups with highest bull growth rate. However, in many of the reports (Rollins *et al.*, 1964; Bradley *et al.*, 1966; Tanner *et al.*, 1969; Wilson *et al.*, 1969; Thrift *et al.*, 1970) breed x sex or sire x sex interactions were not impor-

tant. Added to these, the heritability of postweaning gain for steers in the feedlot and heifers on pasture as estimated by Carter and Kincaid (1959) were 0.38 and 0.54, respectively.

From the review of all these reports, it appears that interactions involving sex are not important after weaning. Probably at this age, variation in sexual dimorphism is less important with an increased influence of other environmental factors.

Yearling Weight.—Heritability estimates from two herds maintained under different nutritional conditions were .42 and -.23; and 0.44 and -0.19, respectively, as reported by Rollins and Wagnon (1958); and Wagnon and Rollins (1959). These figures indicate the presence of herd x nutritional level interactions.

A sire x sex interaction has been found to be an unimportant source of variation in all the reports (Bradley, *et al.*, 1966; Wilson *et al.*, 1969; Thrift *et al.*, 1970). As stated earlier, the sexual dimorphism gradually diminishes after weaning and other environmental effects become more and more important. This shows that progeny testing of sires based on performance of progeny of either sex will be equally effective.

Yearling Score.—As it was for other postweaning traits, genotype x environment interactions, as evidenced by line of sire x year and line of dam x year effects, were not found significant by Urick *et al.* (1968).

Feed Efficiency.—An important economic trait such as feed cost constitutes a major part of the expenses of producing beef. If sires differ in their response to different feeds, performance testing has to be done with feeds which are likely to be used in the ration for the coming generations. It is hard to comply with such a requirement as the type of feed used on a farm is always changing for economic reasons. The situation appears to be more complicated in view of the fact that usually the male yearlings grow in the feedlot, whereas the heifers are maintained on pasture. The presence of interactions will bias, or at least lower, the selection differential if the ranking order does not change. A solution to such a problem is probably not practical. Each such instance may have to be dealt with separately.

The few reports made on the importance of interactions on feed efficiency are illustrated in Table 9. From these reports, genotype x environment interac-

TABLE 9

Genotypes	Environments	Importance of interaction	Author(s)
Hereford sires	Two different rations	Significant	Woodward and Clark (1950)
Black Pied Lowland sires	Fresh and dried feed stuffs	Not important	Haring <i>et al.</i> (1963)
Identical twins of beef breeding	Rations, high and low in concentrates	Significant	Warwick <i>et al.</i> (1964)
Sires of Hereford and Hereford Red-Poll	Steers and heifers	Significant	Bradley <i>et al.</i> (1966)

tions appear to be important for feed efficiency. The presence of sire x sex effects necessitates more thought on the problem of raising bull calves (or steers) and heifers under different conditions of management and feeding.

Carcass Traits and Body Measurements.—Carcass traits are considered to be the most important economically as the sale price of an animal depends on the amount and quality of meat that it yields. From this viewpoint, it is important to determine if interactions exist. Since usually several carcass traits are included in any one report, only a brief review of such reports is included in Table 10:

TABLE 10

Genotypes	Environments	Carcass traits	Significance of interaction	Author(s)
Sires and dams of Angus, Shorthorn, Hereford breeds and their crosses	Years	Carcass wt.	NS	Cundiff <i>et al.</i> (1969)
Black Pied Lowland sires	Fresh and dried feed stuffs	Dressing %	NS	Haring <i>et al.</i> (1963)
Monozygotic twins of beef breeding	Two rations, high and low in concentrates	Marbling score Slaughter wt., carcass wt., carcass grade, rib eye area fat thickness, tenderness, and other traits.	Sig. NS	Warwick <i>et al.</i> (1964)
Angus, Hereford, Brahman breeds and their crosses	Full feeding <u>vs</u> equalized feeding	Tenderness of steak and roast	Sig.	Huffman <i>et al.</i> (1967)
	Papain injection <u>vs</u> control	Tenderness of steak and roast	Sig.	Huffman <i>et al.</i> (1967)
Hereford and Hereford x Red Poll Sires and breed of dam	Steers and heifers	Slaughter grade Carcass wt., dressing %, rib-eye area, fat thickness, tenderness, marbling score, and other traits.	Sig. NS	Bradley <i>et al.</i> (1966)

TABLE 10 (Cont'd.)

Genotypes	Environments	Carcass traits	Significance of interaction	Author(s)
Angus sires	Steers and heifers	Carcass grade, tenderness Carcass wt., LD area, retail yield, marbling score, and other traits.	Sig. NS	Suess <u>et al.</u> (1966)
Angus sires	Bulls, steers and heifers	14 carcass traits including carcass wt.	NS	Tanner <u>et al.</u> (1969)
Hereford sires	Steers and heifers	Carcass wt., rib-eye area fat thickness, marbling score and other traits.	NS	Thrift <u>et al.</u> (1970)
Polled Hereford sires	Steers and heifers	Trimmed loin wt. Carcass wt., dressing %, fat thickness, LD area, marbling score, W-B shear, and other traits. score, W-B shear, and other traits.	Sig. NS	Wilson <u>et al.</u> (1969)
Swedish Friesian and Swedish Red-and-White progeny	Bulls and steers	Subcutaneous fat thickness, internal fat wt., ratio of fore to hind quarter.	h^2 lower in steers than in bulls	Brannang (1967)
Weight groups of Angus cattle	Important muscles of steers and heifers	Extractable lipid % Lipid phosphorus (mg./100 gm.) Total cholesterol (mg./100 gm.)	Sig. NS NS	Terrell <u>et al.</u> (1969)
Weight groups of Angus cattle	Important muscles of steers and heifers	Fatty acids: C ₁₈ ' C ₁₄ :1 of the neutral fraction: C ₁₄ ' C ₁₈ :2 of phospholipid fraction, and others.	Sig. Sig. Sig. NS	Terrell and Bray (1969)

Sig. = Significant; NS = Not significant.

These papers show the variability in results, with no consistency of significance for any character. Further, there have been few studies of interactions involving the same kind of environments. It appears interaction effects are probably not important for carcass traits.

An interesting study on body measurements of identical and fraternal twins at two levels of energy (high and low) was made by Kress *et al.* (1969). The body measurements were: 56-day gains in height at withers, depth of chest, heart girth, circumference of front cannon, length of front leg, length from hooks to pins, width of hooks, width of head, and length of head. Although about 12 percent of the twin sets x diet interactions were significant, in general, none of them appeared to be an important source of variation.

Characters Related to Fertility.—A significant interaction involving two breeds (Hereford and Brahman) and two levels of protein intake for the *interval from first mating to calving* was observed by Howes *et al.* (1963). In addition, a comparison of Hereford, Angus and crossbred heifers raised in two nutritional levels by Wiltbank *et al.* (1969) showed significant breed x nutritional level interaction for both *age and weight at puberty*.

In a study involving six breeding groups of cows, Koger *et al.* (1962) found highly significant breed x lactation and breed x year interactions for per cent calves weaned, which was the same as *per cent calving* in their data.

Significant sire x region interactions were noted for *gestation length* and *difficult calving* by Edwards *et al.* (1966) in their study on the use of Charolais and Hereford bulls on cows of various dairy breeds. Added to these findings, Sagebiel *et al.* (1969) reported significant cow breed x year interactions for dystocia score in female calves. However, none of the interactions, bull breed x year in female calves or cow breed x year and bull breed x year in male calves, were significant for the same trait. The breeds used in their study were: Angus, Charolais, and Hereford.

Cancer Eye in Hereford.—Anderson (1960), while comparing Hereford heifers on three levels of winter feeding, observed an increase in the probability of the development of cancer eye with a high level of nutrition. Since eye lid pigmentation is known to reduce the probability of cancer eye, a genotype x level of nutrition interaction is likely to occur through a change in the threshold level of the combination of genetic and environmental factors. Further research in this aspect, however, is needed to arrive at a definite conclusion.

Vitamin A and Carotenoid Concentration.—Heritability estimates of liver and blood plasma vitamin A and carotenoid concentration were determined by Diven *et al.* (1960) in Hereford bulls and heifers at 230 (period I) and 350 days (period II) of age. Their values with 95 percent confidence intervals are shown in Table 11.

TABLE 11

		Heritability estimates	
		Bulls	Heifers
Period I	Liver		
	vitamin A	0.44 ± 0.49	0.72 ± 0.62
	carotenoid	0.00	0.35 ± 0.52
	Blood plasma		
Period II	vitamin A	0.00	0.25 ± 0.60
	carotenoid	0.13 ± 0.46	0.28 ± 1.24
	vitamin A	0.20 ± 0.48	0.21 ± 0.53
	Liver		
	carotenoid	0.14 ± 0.45	1.32 ± 0.82
	vitamin A	0.00	0.06 ± 0.39
	Blood plasma		
	carotenoid	0.52 ± 0.57	0.26 ± 4.27

Although the 95% confidence intervals included zero for most of the estimates, the trend for higher values associated with heifers is consistent, which has also been noted for heritability estimates of other traits.

Thyroxine Secretion and Distribution—In a study involving Hereford x Shorthorn, Africander x Hereford, and Brahman x Hereford steers, Post (1965) observed no significant breed x month (season) interactions for thyroid secretion rate, plasma protein-bound iodine, extrathyroidal thyroxine, thyroxine volume of distribution and thyroxine turnover rate.

Body Temperature.—Moran (1970) compared the diurnal range of rectal temperatures of $\frac{3}{4}$ —Brahman— $\frac{1}{4}$ —Shorthorn and Hereford steers during winter months in New England and observed a significant breed x time interaction for this response. The results indicated a greater sensitivity of Brahmans to an extremely low temperature.

Dairy Cattle

As stated previously, the environmental conditions to which dairy cattle are exposed are less varied than those to which beef cattle are exposed. This happens because of individual attention that has to be paid to the dairy cattle. In addition, the necessity for maintaining purebred dairy herds results in use of

most of the additive genetic variance through increased intensity of selection. Consequently, the importance of genotype x environment interactions in dairy cattle arises because of selection and testing of bulls in a central place, usually in herds with better management and higher levels of production, for use over herds varying widely in location, management, level of production and so on. In the presence of interactions, the bulls may rank differently in the different herds or at least differ in the relative magnitude of their breeding values, resulting in a difference in the heritability estimates. In either case, the progress would be lower in the existing practice than if the bulls were tested in the herd where they were used. Thus, most of the reports in dairy cattle have been centered on sire x herd interactions or differences in heritability estimates at different production levels.

Milk Yield.—Many of the reports show that sire x herd interactions are not important for milk yield (Hickman and Henderson, 1955; Legates *et al.*, 1956; Wadell and McGilliard, 1959; Van Vleck and Henderson, 1961; Kelleher *et al.*, 1967). It may be noted that the genotypes and the environmental conditions in the herds included in these studies varied widely. In spite of this, the unimportant interaction effects are encouraging. It is not surprising because farming practices for dairy cattle are quite uniform over herds in any one region.

Estimate of heritability is a means of studying the differences in the relative magnitude of the breeding values over different environments, a type of interaction, where the ranking order does not change. In other words, the environmental variance varies from one genotype to the other. This may enhance the within-sire variance, for example, and thereby lower the heritability estimate (Van Vleck and Barr, 1963). The effect of interactions on different methods of estimating heritability has also been stressed by Pirchner (1960). The use of records as unadjusted data, deviations from contemporary averages, or in other forms is also likely to influence the estimate of heritability. For example, the use of deviations is likely to remove most of the environmental effects and their interactions, resulting in a reduction of the error variance as pointed out by Van Vleck (1966) and Lee (1966). However, in the study of Allaire and Gaunt (1955), sire x herd interactions were negligible with unadjusted data but enhanced in contemporary comparisons. Further, on a comparison of the accuracy of various methods of estimating the breeding values of sires used in different herds, Hickman *et al.* (1969) found that the correlation of the breeding values was highest for their own method using herd production and age of the cows. These reports clearly indicate the importance of the way of expressing the data and the method used in estimating the breeding values on the accuracy of detecting the presence of interactions. Heritability estimates for different herd levels of production have been reported. Some of them are listed below in Table 12.

Although the differences were not significant in some of the reports, the trend for higher heritability at higher levels of production is evident. However,

TABLE 12

Particulars of sires	Levels of production in ascending order			Method of estimation	Author(s)
	1	2	3		
A.I. sires in Denmark	0.05	0.15	0.22	Paternal half-sib	Mason and Robertson (1956)
Holstein-Friesian	0.20	0.24	0.19	Intra-sire regression of daughters on dams	Mitchel <i>et al.</i> (1961)
Holstein	0.24	0.33	0.30 ^a	Paternal half-sib	Burnside and Rennie (1961)
Holstein	0.19	0.25	0.28 ^b	Paternal half-sib	Van Vleck (1963)
-----	0.33	0.32	0.35	Daughter-dam regression	Vos (1964)
-----	0.20	0.36		Paternal half-sib	Hartmann (1968)
Holstein-Friesian	0.53	0.47	0.38	Daughter-dam regression	Van Vleck and Bradford (1964)
Holstein-Friesian	0.17	0.25	0.30	Paternal half-sib	Van Vleck and Bradford (1964)

a first three from seven levels.

b first three from four levels.

it may be noted that the levels of production were not the same in the different reports. Other reports indicate no difference in heritability estimates at different phenotypic levels (Touchberry, 1963; Bradford and Van Vleck, 1964). Added to the evidence from these reports, Mason and Robertson (1956) found no significant sire x herd level interactions.

Estimates of genetic correlations or rank correlation coefficients have been reported to be generally high, indicating insignificant interactions with levels of production (for example Robertson *et al.*, 1960; McDaniel and Corley, 1967; Harville and Henderson, 1967; among others). However, Brumby (1961), on testing identical twins in two herd levels observed a genetic correlation of 0.11, indicating interaction as an important source of variation. Probably the environ-

mental differences in this study were larger than those of the other reports mentioned.

Interaction components expressed in percent of total variance have also been generally low or negligible in many of the reports (for example: Legates *et al.*, 1963; Pirchner and Lush, 1959; Van Vleck *et al.*, 1961; Bereskin *et al.*, 1962; Gaunt *et al.*, 1964; Fairchild *et al.*, 1966; among several others).

Van Vleck and Hart (1965) estimated heritability of first-lactation milk yield by daughter-dam regression method with daughters and dams in the same and different herds. These estimates were 0.42 and 0.40, respectively, suggesting an environmental covariance of 0.01 between records of dams in the same herd and therefore there was no evidence for the possibility of genotype x herd environment interaction.

An important study of sire x region interactions was made by Lytton and Legates (1966), who compared the performances (expressed as deviations from adjusted herd-mate averages) of Holstein sires used in the northern and southern regions of the United States. Although the regions were more widely separated geographically than some of the other studies in the U.S.A., the genetic correlation was close to unity and the interaction variance was zero. These results suggest that the influence of a region is not likely to change the ranking order of the sires.

Interactions involving year effects have also been found to be unimportant sources of variation (for example: Van Vleck *et al.*, 1961 among others).

Studies of effects of interactions involving other types of environments have also been made, which are listed in Table 13.

From the results of all these studies, it can be safely said that interactions involving levels of production, type of housing and other differences in herd environments are unimportant. Importance of genotype x region interaction probably vary with difference in climatic conditions, which again depends on management practices. However there are sufficient data to be particular about interactions involving nutritional levels and feeding conditions. Results from studies with sequences of lactation lead to uncertain conclusions. The consistent association of higher heritability estimates with first lactation is an advantage for early testing of bulls and thus it is not a concern to the breeder.

Butterfat Yield and Percentage.—As for milk yield, much emphasis has also been given to studying the importance of interactions on butterfat yield and percentage butterfat. Sire x herd interactions have been found to be unimportant (Legates *et al.*, 1956; Wadell and McGilliard, 1959; Touchberry *et al.*, 1960). Sire x herd components of variance expressed as a percent of total variance have also been found to be generally low or negligible in importance (Legates *et al.*, 1953; Pirchner and Lush, 1959; Van Vleck *et al.*, 1961; Searle, 1961; Van Vleck and Henderson, 1961; Gaunt *et al.*, 1964). However, in the study of Searle (1963), the cow x herd component was 35 percent for butterfat yield and 9% for butterfat

TABLE 13

Genotypes	Environments	Significance of interaction	Author(s)
Identical twins	Climate	Substantial	Payne and Hancock (1957)
Identical twins in Sweden	2 feeding levels	Sig.	Bonnier <i>et al.</i> (1948)
Identical twins in New Zealand	3 feeding levels	Unimportant (high rank correlation)	Hancock (1953a)
Identical twins in New Zealand	Meal feeding and no meal feeding before parturition	Sig.	Hancock (1953b)
Identical twins in New Zealand	Periods after calving following meal feeding	Sig.	Hancock (1953b)
Identical twins in New Zealand	Turnips <i>vs</i> silage feeding in the declining phase of lactation	Sig.	Hancock (1953b)
Identical twins in New Zealand	Periods (weeks) in the above mentioned environment	Sig.	Hancock (1953b)
A.I. sires in Sweden	Herds in different planes of nutrition	Unimportant (no difference in h^2 estimates)	Korkman (1953)
Identical and fraternal Holstein twins	High and low grain rations	NS	Freeman (1969)
A.I. sires in Canada	Grain feeding level in summer Grain feeding level in winter, forage feeding conditions in summer, forage feeding conditions in winter, cow exercise, breeding program, milk markets, housing system.	Sig. NS	Mao (1969)
Holstein and Guernsey sires	Herds classified by levels of production, location, days dry, calving interval, type of housing.	NS	Burdick and McGilliard (1963)

TABLE 13 (Cont'd.)

Genotypes	Environments	Significance of interaction	Author(s)
Holstein sires	2 types of housing (stanchions and free stalls)	Unimportant (r_g close to unity)	Miggans and Van Vleck (1970)
Slow and free milking identical twins in New Zealand	Poor vs normal preparation for milking	Substantial interaction	Brumby (1956)
Identical twins in New Zealand	Two pre-milking stimuli	Substantial interaction	Phillips (1960)
Six main dairy breeds in England and Wales	1st and 2nd lactation	Indication of important interaction (h^2 for 70-day and 305 day milk yield 0.35, 0.43; and 0.09, 0.24 respectively)	Rendel <i>et al.</i> (1957)
Swedish Red-and White; Swedish Friesian and Swedish Polled cows	Sequence of lactation	NS (although h^2 higher in 1st lactation)	Hansson and During (1961)
Identical twins in Sweden	Stage of lactation	Sig. in all 3 lactations	Bonnier <i>et al.</i> (1948)

Sig. = Significant; NS = Not significant.

percentage. These high estimates might be due to the fact that only certain selected cows were transferred to other herds, as stated by the author, which resulted in confounding of other interactions such as level of production x herd environments. Nevertheless, further studies on cow x herd interactions are required to arrive at an accurate conclusion. Added to these findings on sire x herd interactions, the genetic correlation of breeding values of Holstein sires used in the northern and southern regions of the United States was found to be close to unity by Lytton and Legates (1966) and a correlation close to unity was also observed by Harville and Henderson (1967) on performances of Holstein sires in different herds. From all these reports, sire x herd interaction appears to be an important source of variation.

Estimates of heritability for butterfat yield and/or percentage have been reported for herds at different levels of production. In some of the reports a

definite trend of increase in the estimate with an increase in the level of production has been observed (Johansson, 1953; Mason, 1954; Mason and Robertson, 1956; Gravert, 1958; Touchberry, 1963; Van Vleck, 1963). Although the differences in heritability estimates were not significant in some of the reports, the trend was consistent. However, no such relationship between heritability and level of production was observed in other reports (Legates, 1957; Mitchell *et al.*, 1961; Legates, 1962; Fairchild *et al.*, 1963; Vos, 1964). In the study of Mason and Robertson (1956) the ranking order of the bulls in different herds remained the same and the sire x herd level interaction was also negligible. The results of all these reports indicate the insignificance of sire x herd level effect as a source of variation. The trend for higher heritability estimates with a higher level of production need not concern the breeder as usually sires are selected from herds with higher levels of production.

Bonnier *et al.* (1948), using identical twins, observed significant interactions with two feeding levels for fat percentage in all three lactations. Their results were supported by the findings of Hancock (1953b), who also observed significant interactions of identical twin sets with meal feeding *vs* control feeding. However, in the same experiment, the interaction was not significant for butterfat yield. In another experiment, Hancock (1953b) fed turnips or silage to the identical twin sets and found highly significant interactions for butterfat yield but contrary to this finding, the same author observed a high rank correlation between sets in three feeding levels in an earlier study. The differences in the results of his several trials were probably due to the type of feed and its nutritional value. The physiological condition of the animals at the time of experiment also varied a great deal. Added to these two reports involving identical twins, Korkman (1953) observed no difference in heritability estimates among herds on different planes of nutrition. As the results of these reports vary widely, further research on this aspect is suggested.

Heritability estimates of butterfat percentage in first and second lactations of main dairy breeds in England and Wales were estimated to be 0.43 and 0.42 (Rendel *et al.*, 1957), indicating the unimportance of interactions with sequence of lactation.

Finally, substantial interactions with pre-milking stimuli have been demonstrated in the study of Phillips (1960) using 13 sets of identical twin cows.

Growth Characteristics.—Bonnier *et al.* (1948), while studying the effect of two levels of nutrition on monozygous twins, observed significant interactions on growth in body weight from 1-27 months of age. In the same experiment, age x twin set interactions were also found to be important. But for the increase in height at shoulders, sets x feeding level was not significant and sets x age effect was significant in only one out of the two experiments and the controls. However, Hansson *et al.* (1953) found no significant interaction of intensity of feeding with identical twin sets on growth from 1-25 months of age, although sets x age effects were important.

In other studies involving identical twins and widely different feeding levels, Hancock (1953b) observed significant sets x feeding level interactions as well as sets x period interactions on body weight (means of 4 consecutive weekly weights after calving), but pairs x ration effect was small or negligible in the study of Freeman (1969). In addition to these reports, a differential response of calves sired by Ayrshire bulls to two different rations was seen by Varo (1962) on growth traits, although with Holstein fraternal twins, Burnside *et al.* (1969) found no significant pair x ration interaction on growth in body weight, heart girth, and height from two days of age to 285 lb. live weight. These reports indicate some differential response of genotypes to nutritional levels on growth in body weight but interaction effects on other growth traits are probably not important.

Respiratory Rate.—Interactions involving feeding levels as well as age on respiratory rate were present among sets of identical twins as observed by Hansson *et al.* (1953).

Evaporation from Skin Surface.—Measurements of evaporation from the skin surface from two Zebu breeds, *viz.*, Hariana and Gir in three different seasons made by Joshi *et al.* (1968) indicated important breed x season interactions but breed x location (shoulder, rump, *etc.*) effects were not important.

Traits Related to Fertility in Females.—Genotype x station effects on *conception interval* (service period) are unimportant as indicated by a high correlation among progeny groups of Ayrshire bulls at different stations (Pearson, 1965).

Indications of interaction effects on *conception rate* were seen in the study of Inskip *et al.* (1961) involving Holstein Friesian sire progeny groups and parity (heifers *vs* parous cows) of the daughters. Likewise, genetic differences for the same trait were found to be expressed only in unfavorable environments but not when conditions were favorable among groups of paternal half-sibs, indicating a genotype x environment interaction (Hahn, 1964).

Quiet ovulation in Holstein cattle is also influenced by mating system x parity interactions as observed by Labhsetwar *et al.* (1963).

Semen Quality.—In a 4 x 4 factorial experiment involving four glycerol levels and four equilibration times in freezing semen from eight bulls (two Jersey, three Holstein, one Guernsey, and two Hereford) in liquid nitrogen vapor, *post-thawing motility* was significantly influenced by bulls x glycerol levels and bulls x equilibration time effects (Roussel *et al.*, 1964). This indicates a differential response of bulls to various glycerol levels and equilibration time and thus the determination of the correct glycerol level and equilibration time for each bull in any A.I. center would be profitable.

Buttle *et al.* (1965) studied the effects of factors such as phase contrast and direct microscopy, staining with nigrosin or nigrosin-eosin, and treatment with sodium fluoride (which is necessary to immobilize the sperm for the phase contrast method) and without this treatment on *counting of dead spermatozoa* in frozen semen in a factorial design. Significant bull x fluoride treatment and bull x

staining method interactions suggest the use of only the method which would give the least variable results.

Sheep

The environmental conditions to which sheep are exposed under usual farm practices are comparable to those of beef cattle. There is considerable variation in the type of housing, feeding conditions, systems of management, and such other factors among different regions, including the confounded climatic and altitude effects. Thus, genotype x environmental interactions in sheep are likely to be more important than those in some of the other farm animals such as dairy cattle and poultry. A discussion of the reports on various traits of economic importance follows.

Birth Weight.—Besides the environmental factors mentioned for beef cattle, birth weight in sheep is also affected by the number of lambs born together. Sire x flock (locations) effects were found to be negligible by Radomska (1965); and Osman and Bradford (1965), although in the latter study it was significant in one of the years. Studies of interactions involving blood group genotypes and locations by Stansfield *et al.* (1964) also indicated the absence of such interaction effects on birth weight. Strain x location and strain x year interactions were also found to be nonsignificant by Dunlop (1963). However, interaction effects were found to be significant, when Carter *et al.* (1967) compared the performance of ewes of two breeding groups at two widely separated geographical regions, Virginia in the United States and Quebec in Canada. These results indicate the increased probability of interaction effects with widely separated locations.

In a study by Stakan *et al.* (1963) involving two groups of lambs reared on two planes of nutrition, high and low, heritability estimates were 15.0 percent and 5.4 percent respectively. The higher heritability estimate justifies selection of animals for birth weight on a high plane of nutrition, although more studies need to be made to confirm their results.

As with beef cattle, interactions involving sex are also important in sheep in view of the fact that most of the traits of economic importance are expressed in either sex. However, the few studies reported do not indicate any important interactions involving sex for this trait. Brown *et al.* (1961) noticed no significant line x sex effects; they also found no difference in the heritability estimates or in sire x sex interactions in the study of Vesely and Robinson (1969) in Rambouillet and Romnelet breeds. Only low heritability estimates, .00 and .04, for male and female lambs, respectively, were reported by Taneja (1968). Although the reports are few, interactions involving sex do not appear to be important for birth weight in sheep.

Average Daily Gain (A.D.G.) (Birth to Weaning).—Again, because of the relatively more frequent occurrence of twinning in sheep as compared to beef cattle, the A.D.G. in the former is likely to be more variable. Positive interac-

tions involving sires and flocks were noted in the study of Radomska (1965). Such an interaction effect was found significant by Carter *et al.* (1967) while comparing the performances of two breeding groups of ewes in Virginia (U.S.A.) and Quebec (Canada). The genotypes and environments in the latter study differed more widely than those in the former.

Important line x sex interactions were observed by Brown *et al.* (1961) for number of days required to reach 60 pounds. But sire x sex effects were unimportant except during one year in the Rambouillets as reported by Vesely and Robinson (1969). In the latter study, the heritability estimates in the two sexes were also the same. These reports indicate the importance of interactions involving sex when the groups to be compared are wider apart genetically.

No differential response of three breeds of sheep (Rambouillet, Targhee, and Columbia) to two ages at weaning (75 and 125 days) was noticed by Ercanbrack and Price (1969), indicating that the daily gains at an earlier age could be used for purposes of selection.

Weaning Weight.—The age to which weaning weights of lambs are adjusted varies a great deal from one region to another although generally it is around 120 days. Thus, results are likely to vary to some extent from one report to another. In a study involving five strains of Australian Merinos, Dunlop (1963) found no significant strain x year or strain x location interactions. Sire x flock (location) effects were also found to be nonsignificant by Osman and Bradford (1965). Similar results have been reported by Stansfield *et al.* (1964) from a comparison of the blood-group genotypes (alleles at 7 loci) at two locations. However, weaning weight was significantly influenced by breeding group x region (Virginia in U.S.A. and Quebec in Canada) interactions (Carter *et al.*, 1967). Again, it may be noted that the differences in the genotypes and the environments were greater in the last report as compared to those in the other studies and this probably was responsible for the differences in the results. Added to this, the presence of a sire x station (testing station *vs* flocks) interaction was noted by Radomska (1965).

Line x sex and sire x sex effects were unimportant for weaning weights as reported by Brown *et al.* (1961) and Vesely and Robinson (1969), respectively. In the latter study, differences in the heritability estimates for the two sexes were also negligible. From these reports, interactions involving sex and weaning weight appear to have no significance in sheep.

Yearling and Adult Weights.—As is true with any market animal, yearling weights in sheep are important from the business standpoint. The presence of interactions would hamper the genetic progress, unless properly accounted for. In the Australian Merino, Dunlop (1963) observed nonsignificant strain x year and strain x flock interactions for adult weights. However, Radomska (1965) noted the presence of sire x flock effects in development to 12 months of age in ewe lambs; such interaction effects were found highly significant (from pooled mean squares) for 450-day weights by Osman and Bradford (1965).

Experiments to determine interactions with different nutritional levels have shown variable results. The reports are summarized in Table 14.

TABLE 14

Genotypes	Environments	Carcass traits	Significance of interaction	Author(s)
Blackface, Cheviot and Wiltshire Hogs	2 planes of nutrition (high and low)	Yearling weight	NS	King and Young (1955)
Blackface, Cheviot and Wiltshire Hogs	Cold and warm temperatures	Yearling weight	NS	King and Young (1955)
Australian Merino half-sibs	2 planes of nutrition (high and low)	12-month wt. 17-month wt.	Sig. $r_g = .16$ Sig. $r_g = .29$	Morley (1956)
Twin lambs of 2 breeds and 5 crosses	High-high, high-low, low-high, and low-low planes of nutrition	Yearling wt.	NS	King et al. (1959)
Fleece plus, random and fleece minus selection flocks	3 levels of nutrition (high, intermediate and low)	Adult wt.	NS	Williams and Winston (1965)
Grade Targhee ram lambs and wethers	2 rations, high and low in energy	Postweaning A.D.G. (period I) Final wt.	Sig. NS	Osman and Bradford (1967)
Rambouillet and Romnelet sires		126-day postweaning wt.	NS (except one group in Rambouillet)	Vosely and Robison (1969)

Sig. = Significant; NS = Not significant.

These results present variable results. However, there are sufficient indications to discourage selection of rams in one flock for use in another flock, especially if they are managed at different nutritional levels.

Carcass Traits.—In meat animals, carcass traits are always considered to be economically important as the ultimate sale price of an animal depends entirely on the quality as well as the quantity of carcass and its constituent parts. Thus, it is necessary to determine if a differential response of genotypes to environments exists for these traits.

Breed cross of ewe x region (Virginia in U.S.A. and Quebec in Canada) interactions were found to be important for carcass weight, carcass yield, weight of leg, loin and rack, and weight of shoulder, neck and breast by Carter *et al.* (1967).

Osman and Bradford (1967), in comparing grade Targhee lambs at two levels of nutrition, observed no significant sire x plane of nutrition interactions for any of the carcass traits (carcass wt., dressing percent, carcass grade, loin-eye area and percentage of fat in carcass) except for carcass weight in ram lambs. Another report involving different levels of nutrition but with various breeding stocks was made by King *et al.* (1959), who observed significant interaction effects for weight of cannon bone but not for carcass wt., chest circumference, eye muscle (width x depth), depth of fat over eye muscle and other cannon bone measurements. Thus, interactions with nutritional regimes for carcass traits do not appear to be important, although further studies need to be made to confirm such a conclusion.

Sire x sex interactions were investigated by Cramer and Marchello (1964) for iodine number, melting point, lauric acid, myristic acid, palmitic acid, stearic acid, oleic acid, linoleic acid and minor acids from fat biopsies from six bisexual Columbia twin pairs from 9 weeks to 18 months of age. Except for iodine number, interactions were not significant for any other trait. In another study, significant line of breeding x sex (wether and ram lambs) interactions were seen for carcass weight, fat percent, and protein percent but not for fat:protein ratio (Kromann and Ray, 1967). The results of these reports vary in indicating interactions involving sex. Therefore, further studies on this aspect are suggested.

Feed Intake.—Significant sire x energy level (two rations) interactions were observed among grade Targhee lambs and Osman and Bradford (1967). Interaction effects involving three levels of nutrition (low, intermediate and high) and three selection flocks (fleece plus, random and fleece minus) were also found significant by Williams and Winston (1965). In addition, the presence of breed x pasture effects was noticed by Langlands (1968). All of these reports consistently indicate the differential response of genotypes to different feeding conditions for feed intake. This may be the reason why important interactions involving nutritional levels were noted for many of the traits of economic importance.

Milk Yield.—In an analysis of 58,381 lactations of Lacaune ewes in 58 flocks, Romer *et al.* (1969) estimated the flock x year interaction components for milk yield during the milking period, duration of the milking period, and milk yield up to the peak record, 4.4, 7.1, and 6.8 percent, respectively.

Fleece Characteristics.—The quality and yield of wool are considered to be most important economic traits in the sheep business as they determine the percent return to a great extent. Therefore, interaction effects, if any, have to be carefully considered. The constituent traits in wool production are many, and they vary a great deal among the various reports. Thus, to discuss them concisely they are listed in Table 15.

It may seem that these reports present variable results. The importance of interaction effects on wool and fleece traits appear to depend on the differences in the genotypes and also the environments in an experiment. Thus, it becomes necessary to determine the importance of interaction effects shown by the genotypes and the environments separately for each case to make breeding plans effective.

Reproductive Traits in Ewes.—The success of livestock breeding depends to a great extent on the size of the crop of young at birth and their ability to survive and grow to market age. From this viewpoint, reproduction traits, especially in females (because of lower selection intensity) are to be considered most important from the production standpoint. Therefore, interaction effects on these traits need special consideration, particularly when they are known to be influenced greatly by breeds or strains and a variety of environmental differences.

Dunlop (1963), in a comparison of 5 strains of Australian Merino sheep in 3 regions, found no significant strain x location or strain x year effects either in *number of lambs born* or *number weaned*. Flock (wt. +, random bred and wt. -) x year effects were also found to be nonsignificant by Pattie (1965) for *wet ewes*, *lambs mothered*, *lambs weaned* (all three expressed as percent of ewes joined), *multiple births*, *ewes lambled and lost* (both expressed as percent of wet ewes) and *lamb deaths* (mothering to weaning as percent of lambs mothered). However, Dun *et al.* (1966) noticed significant strain x season interactions for *percentage of ewes lambing* (as a percent of ewes joined) and *twin births* (as percent of lambing ewes) but not for first services (as percent of ewes joined) in a comparison of autumn and spring joining ewes of two strains, Peppin and South Australian Merinos. The significant interactions with seasons (but not with years) as seen from these reports are not surprising as sheep are known to vary in their seasonal pattern for reproduction. Further, in a study involving 5 strains of Merinos at 3 locations, no significant strain x location or strain x age or strain x sex interactions were noticed for survival rate to weaning of single lambs by Lax and Turner (1965). However, Carter *et al.* (1967), in their study on the performances of two breeding groups in the U.S.A. (Virginia) and Canada (Quebec), observed significant breed cross of ewe x region interactions for pounds of lamb weaned per ewe mated, average lambing date, and ewes lambing of ewes mated. These studies, along with that of Dunlop (1963), indicate the importance of interaction effects for reproductive traits with larger differences in the genotypes as well as in the environments involved in an experiment.

TABLE 15

Genotypes	Environments	Trait(s)	Significance of interaction	Author(s)
5 strains of Australian Merino	Locations	Clean fleece wt., greasy fleecy wt., % clean scoured yield, character, color, crimps per inch, fibre diameter, staple length. Fibres per mm ² , count, sound- ness, handle.	Sig. but components were small NS	Dunlop (1962)
	Years	As listed above	Sig. only for clean scoured yield and fibre diameter	
Sires in 5 strains of Australian Merino	Locations	Clean fleece wt.	NS	Dunlop and Young (1966)
	Drops Years	Clean fleece wt. Clean fleece wt.	NS NS	
Blood group genotypes (7 loci)	2 locations	Side wool grade, thigh wool grade and staple length at weaning; grease fleece wt., staple length and fleece grade of yearlings	NS	Stansfield <i>et al.</i> (1964)
Merino sires	Flocks and progeny test- ing station ♀♀ only	Wool fineness at 2nd shearing	Sig.	Radomska (1965)
		Fleece wt. and other wool and fleece characters	NS	

TABLE 15 (Cont'd.)

Genotypes	Environments	Trait(s)	Significance of interaction	Author(s)
Whiteface Targhee type sires	2 locations	Staple length Grease fleece wt., fleece grade, face score (degree of wool covering)	Sig. (pooled estimate) NS	Osman and Bradford (1965)
2 breeding groups	2 regions (Virginia in U.S.A. and Quebec in Canada)	Fleece wt.	Sig.	Carter <i>et al.</i> (1967)
Blackface, Cheviot and Wiltshire Hoggs	2 planes of nutrition	Clean wt. of all fibres on tat- toed area, clean wt. of wool fibres on tattooed area. Density (fibres per unit area), density (non- medulated fibres per unit area) average length of all fibres, average diameter of all fibres, average diameter of wool fibres	Sig. NS	King and Young (1955)
Australian Merino sires	2 planes of nutrition (high and low)	Greasy fleece wt., yield, clean fleece wt., staple length and crimps per inch.	NS	Morley (1956)
Twin lambs of 2 breeds and 5 crosses	High-high, high-low, and low-high planes of nutrition	Greasy wool wt. and fibre length	NS (no dif- ference in h^2 estimates either)	King <i>et al.</i> (1959)
Sires of fine- wooled sheep	2 planes of nutrition (high and low)	Fleece wt.	h^2 : 19.8 and 19.4% respectively	Staken <i>et al.</i> (1963)

TABLE 15 (Cont'd.)

Genotypes	Environments	Trait(s)	Significance of interaction	Author(s)
Fleece plus, random and fleece minus flocks	3 levels of nutrition (low, intermediate and high)	Clean dry wool Efficiency (g wool: g food)	Sig. NS	Williams and (1965)
Fine wool, medium wool and strong wool strains of Merino	2 levels of nutrition (different proportions of fodders) Planes of nutrition	Efficiency of conversion of fodder to wool Wool characters in general	NS ($r_g = 0.89$ on within strain basis) h^2 lower in low plane	Dunlop <u>et al.</u> Stakan (1966)
Grade Targhee ram and wether lambs from different sires	High and low energy rations	Staple length in period I, clean fleece in period II	Sig.	Osman and Bradford (1967)

Sig. = Significant; NS = Not significant.

Ch'ang (1963) studied the response of Romney Marsh ewes born as singles or twins when grazed on an estrogenic red clover sward and on a control pasture. The genotype x pasture interactions were not significant for date of lambing, but, however, were significant for percent barrenness (as a measure of lambing percentage) in one year.

Based on the results of only one report, it is not safe to draw any conclusion. Further research on interactions involving differences in feeding conditions for reproductive traits are suggested.

Blood Characteristics.—The study of King *et al.* (1959), dealt with twin lambs of two breeds (Blackface and Welsh Mountain) and 5 crosses by four nutritional environments (high-high, high-low, low-high, and low-low), thus involving two periods. They found significant cross x plane of nutrition interactions for N.P.N. (mg./100)² but not for Hb, total protein, alb./glob. ratio, sugars, inorganic phosphate, and serum alkaline phosphatase in period I. These results indicate a differential response of the genotypes to different planes of nutrition and so the necessity of using uniform genotypes in nutritional experimental designs is felt.

Worm Infestation.—Emik and Gregory (1947) made counts of *trichostrongyloid* worm eggs in fecal samples of male and female lambs of various mutton and wool breeds. A highly significant sex x type mutton or wool interaction was

observed in response to worm infestation. As stated by the authors, the females were responsible for most of the differences. In view of this, it would be interesting to see if a difference in the heritability estimates for worm infestation exists between the sexes. They added that the breed x sex interaction was significant when corrected for type, indicating differential resistance of breeds within types. However, no breed x plane of nutrition effects were noticed by King and Young (1955) in worm egg and larval counts of three breeds (Blackface, Cheviot, and Wiltshire Hogs) reared on two planes of nutrition (low and high). The reports are too few to draw any conclusion. Nevertheless, the interesting observation on type x sex interaction should stimulate further research on this trait.

Acclimatization to Cool Temperatures.—Sykes and Slee (1969) exposed South-down and Welsh Mountain 1-yr-old ♀ ♀ sheep reared on two planes of nutrition (low and high) to -20°C with 4 m.p.h. wind for 100 min. twice after a previous exposure of half the sheep to 8°C and the other half to 30°C for two weeks each time. No significant breed x temperature (previous exposure) or breed x nutrition effects were observed, although the breed x plane x temperature (previous treatment) for change in rate between first and second exposure was significant at $P \leq .05$. These results indicate the differential response of breeds to combinations of plane of nutrition and previous exposure to acclimatization.

Swine

As with other market animals, the environmental factors, such as method of housing, feedlot conditions, and other management practices, including castration effects, vary greatly in different regions. Thus, the presence of interactions will lower the effectiveness of selection if animals are selected in one environment and used for breeding in another. Added to these factors, litter size and milk production in sows greatly influence individual pig weights and the litter weights. Therefore, a prior investigation of the presence of interactions is a must before production practices are recommended for the various genotypes. Most of the reports on interactions in this species have been on postweaning performance and carcass traits and only a very few reports have been made on preweaning traits.

Litter Size.—From data on five breeds of swine, Quijandria *et al.* (1969) observed significant breed x year but not breed x season interaction effects. Although the results indicate a differential response of the breeds to years but not to seasons, it is not safe to draw any broad conclusion from this single report. Further research on this aspect is needed.

Litter Weight at Weaning.—A sire x season interaction effect was reported to be nonsignificant by Zoellner *et al.* (1963) in their data on Poland China pigs. Again, as this was the only report available on litter weaning weight, further investigations are necessary to draw any inference.

Postweaning Performance.—Except for carry-over effects of litter size and milk production of sows, if any, postweaning performances are influenced solely by

other environmental factors. Moreover, the market price of an animal largely depends on its postweaning performance. This may be the reason why most of the attention on the study of interactions was on these traits.

Breed x year effects were found significant for average daily gain (A.D.G.) and feed conversion by Quijandria *et al.* (1969) in a study of five breeds of swine (Duroc, Yorkshire, Hampshire, Poland, and Spotted). However, in the same study, breed x season interactions were important for A.D.G. but not for feed conversion. Another study reporting sire x season effects was made by Zoellner (1963), where significant interactions were not found for either A.D.G. or litter feed efficiency.

Research on interaction effects involving nutritional differences appears to have drawn more attention than research on any other environmental effects. However, a special mention of the work of Fowler and Ensminger (1960) has to be made in view of the fact that it was similar to that of Falconer and Latyszewski (1952) in estimating the importance of interactions from direct and correlated responses. After a few generations of selection of swine for rate of gain on high (H) and low (L) planes (full feeding *vs* restricted feeding) of nutrition, they (Fowler and Ensminger, 1960) transferred half of each line to the other line. Thus, estimation of direct and correlated responses in both planes was possible from the four groups: HH, HL, LH and LL. Those in the LH group were more efficient in feed utilization and gained faster than the HH pigs; whereas, the HL group gained slower and consumed more feed per pound of gain than those in the LL group. These results support the contention of Falconer (1952) that animals should be selected in the environment in which the progeny are likely to perform. Such a conclusion was further supported by the nonsignificant difference of the heritability estimates on the two planes of nutrition. The importance of interactions in their study was further demonstrated from the pooled estimate of r_g , which was 0.70. Significant genotype x level of feeding (full *vs* restricted) effects were also found in the studies of Lindgren *et al.* (1932) (big type *vs* chunky type) for feed efficiency, Donald (1940) for growth rate, Warren and Dickerson (1952) for live weight gains, Lucas and Calder (1956) for live weight gains and feed efficiency, Salmella *et al.* (1960) for rate of gain in the feedlot and age at 200 pound but not for feed per 100 pounds gain and Fowler and Ensminger (1951) for live weight gains. However, interactions involving feeding levels were not found significant by Gregory and Dickerson (1952) for live weight gain and Hale and Coey (1963) for live weight gain and food conversion rate. It may be noted that the genotypes in these studies were different. Moreover, differences in appetite and efficiency of the animals would be reflected in full feeding and restricted feeding. The results of these reports produce sufficient evidence in support of the differential response of genotypes to high and low feeding levels. Therefore, it will be appropriate to select animals in a feeding level in which the progeny are expected to perform.

Interactions of various genotypes with other nutritional differences have also been studied. Plank and Berg (1963), in comparing sires of three breeds of swine (Yorkshire, Lacombe and Landrace), observed significant sire x feeding level (equalized *vs* liberalized feeding) interactions for average daily feed consumed and A.D.G. but not for feed per pound of gain.

Other studies include significant breed (Landrace, Pietrain and their crosses) x diet (low *vs* high crude fibre) effects for feed intake and A.D.G. noticed by Duckworth *et al.* (1966); important breed (Duroc and Hampshire) x dietary fat level as well as breed x dietary energy level effects on A.D.G. observed by Hale *et al.* (1967); differential response of three breeding groups to two diets, high and low in digestible energy, for feed consumption and A.D.G. reported by Skitsko and Bowland (1970); a significant influence of ration (2 energy levels and 2 protein levels) x strain (4 strains of bacon hogs) effects on A.D.G. and average daily feed intake in growing period and feed efficiency in the finishing phase (but not for feed efficiency) in growing period or A.D.G. and average daily feed in the finishing period observed by Bouland and Berg, 1959; important breed (Duroc and Hampshire) x protein level (3 levels) effects on feed efficiency found by Hale and Southwell (1967); nonsignificant interactions of three crosses with two rations (conventional *vs* high growth) for A.D.G., food conversion ratio, and food consumption observed by King (1963); significant litter (Dutch Landrace pigs) x ration (breeding and fattening) effects on feed consumption reported by Kroeske (1968); and different reactions of inbred lines (Poland China) and their crosses to feeding treatments (pasture and dry lot) observed by Weaver and Bogart (1944). However, when pigs were self-fed the same feed in dry lot and in pasture, the sire (Canadian Yorkshire) x treatment interaction only approached significance ($P = .09$).

These reports do present sufficient evidence for differential response of genotypes to various nutritional differences, both in quality and quantity, and further emphasize the necessity of selecting animals in an environment in which they are to live and perform.

Heritability estimates for A.D.G. and/or feed efficiency, as estimated from Danish pig testing records, were found to be consistently higher under individual feeding than under group feeding (Jonsson, 1955; Fredeen and Jonsson, 1957; Jonsson, 1959a; Jonsson, 1959b). One of the explanations suggested by the authors was that under individual feeding, the within-litter variance was lowered due to reduced competition among litter mates. However, the genetic correlation estimated by Jonsson (1959b) was 0.925, indicating that the breed x type of feeding interactions were unimportant. Nevertheless, the results do suggest that selection would be more effective under individual feeding.

Ollivier (1965) compared the performance of boars from three breeds (Large White, Normandy and Pietrain) in a piggery, heated in winter, with individual stalls, and 3 meals daily according to appetite *vs* performance in an open-air enclosure with straw bales for shade in summer and wire netting pens to hold

three animals fed twice daily to appetite. On a within-breed basis, the sire x environment interaction was highly significant for A.D.G. among the Normandy pigs. As regards breed x environment interactions, only the Large Whites showed a marked reduction in A.D.G. under unfavorable conditions in the piggery as compared to Pietrains. These results indicate the differential response of sires and breeds to type of housing.

Differential responses of genotypes to sex have also received considerable attention. Winters *et al.* (1942) compared the sexual dimorphism shown by barrows and boars for growth rate from 8 to 24 weeks in Poland China and Minnesota No. 1 swine, which were significantly different. Their results (rearranged) are shown below as an example.

		Increase in weight by age and groups				
		8	12 ^a	16	20 ^a	24 ^a
Difference, lb. (barrow-boar)	Poland China	-.96	-2.33	-3.19	-3.26	-3.62
	Minn. No. 1	-2.16	-7.52	-2.74	10.74	21.40

a Significantly different sexual dimorphism between breeds

Next in the series of their reports, Comstock *et al.* (1944) compared barrows and gilts. Although the sex x sire interaction for postweaning growth rate was negligible within Poland China lines, it was significant in Minnesota No. 1, as was the breed x sex interaction. Further, Bouland and Berg (1959) noted the presence of strain x sex effects on A.D.G. both in growing and finishing periods.

A coefficient of genetic correlation between sexes (barrows and gilts of Landrace), significantly different from unity was observed for A.D.G. but not for feed efficiency or feed consumption by Smith and Ross (1965), indicating a significant sire x sex interaction for A.D.G. However, heritability estimates for each sex differed significantly only for feed intake per day at 200 pound live weight. Added to these evidences, breed x sex interactions were significant for A.D.G. but not for feed conversion in the data of Quijandria *et al.* (1969). However, interactions involving sex were not found to be important by Kristjansson (1957) for A.D.G. (male and female pigs); Omtvedt *et al.* (1962) for A.D.G. (barrows *vs* gilts); Hale and Coey (1963) for A.D.G. and feed conversion rate (barrows *vs* gilts); Plank and Berg (1963) for A.D.G., feed intake and feed efficiency (barrows and gilts); Magee (1964) for 154-day weight, the interaction being inbreeding x sex (barrows *vs* gilts) (though nonsignificant, estimate of the size of interaction was 2 lb.); Omtvedt and Jesse (1968) for A.D.G. and feed efficiency (boars, barrows and gilts); and McGloughlin (1968) for A.D.G. (Landrace barrows and gilts; r_g close to 1).

Many of the reports did not indicate any importance of interactions involving sex for postweaning performance. However, in view of the few significant results, there should be a determination made of the influence of genotype x sex interactions in each case where selection of breeding animals is involved. It may be noted that the genotypes in some of the references were not described here and may be referred to under genotype x nutrition interactions.

Carcass Traits.—As mentioned earlier under beef cattle and sheep, carcass traits in market animals are always considered most important from the business standpoint, and thus, necessitate investigations on the genotype x environment interaction effects. Usually, investigations include many carcass traits and they vary a great deal from one report to the other. Therefore, these will be reviewed as concisely as possible.

Breed x year effects in the study of Quijandria *et al.* (1969) were significant for loin-eye area, percent lean cuts, average carcass backfat, backfat at last rib and last lumbar, percent primal cuts-live weight, percent ham, percent loin and percent shoulder but not for slaughter weight, backfat last rib and dressing percent. In the same report, breed x season effects were significant for slaughter weight, percent lean cuts, backfat-average and at the last rib, and the percent shoulder. Breed x year effects were not important for other traits.

Zoellner *et al.* (1963) observed no significant sire x season effects on average backfat thickness. Although only a few reports on interactions involving year and season effects have been made, the results do indicate the possibility of their occurrence.

Most of the reports on interaction effects for carcass traits involve full and restricted feeding. They are: indication of the presence of interactions in some measures of carcass quality by Lindgren *et al.*, 1932; presence of interactions for backfat thickness (pigs from Essex Saddle Back and Large Black sows, sired by the same Large White boar) in the study of Fishwick (1936); nonsignificance for any of the carcass traits (three breeds in four different combinations of feeding) studied by Cummings and Winters (1951); unimportant response for the carcass traits observed by Warren and Dickerson (1952) but important as reported by Gregory and Dickerson (1952); significant for many carcass traits in one experiment but in another experiment with less restriction in feeding, important for only fat measurements (Lucas and Calder, 1956); differential response of crosses of large White and Minnesota breeds to different nutritional treatments (Cole, 1957); significant interactions in length of carcass, ham weights and loin-eye area at the 10th rib (Salmella, 1958); important interactions (selection experiment on high and low planes of nutrition) in primal cuts but none in eye-muscle area or fat thickness noted by Brunstad and Fowler (1959); absence of interactions in all the traits analyzed by Hale and Coey (1963); and nonsignificant sire (German Improved Landrace) x feeding regime interactions in all the traits studied by Nitzsche and Englisch (1967) except for back muscle area in

one trial. The results, though variable, indicate the importance of interactions involving different feeding levels.

Bouland and Berg (1959) found no significant strain x ration (2 protein levels and two energy levels in experiment 2) interactions for any of the characters they studied. Therefore, further investigations of the presence of interaction effects involving different protein levels are needed to confirm their findings.

The line of breeding x management (pasture *vs* confinement) effects were found to be important in dressing percent and carcass backfat in different trials but not for any of the other carcass traits reported by Omtvedt *et al.* (1962). However, Kristjansson (1957) observed significant sire x treatment interactions in loin area, when the same feed was self-fed in a piggery and on pasture.

With equalized and liberalized feeding as treatments, Plank and Berg (1963) found significant sire x treatment interactions in carcass length and total R.O.P. score but none in other carcass traits.

No differential response of sires within breeds to pigs housed individually or in groups of three (details previously reviewed) in any of the carcass traits was observed by Ollivier (1966). However, heritability estimates were found by Fredeen and Jonsson (1957) to be higher under individual feeding as compared to group feeding for backfat thickness and carcass length. The same explanation mentioned under postweaning performance applies here as well. However, a genetic correlation of 0.997 was estimated by Jonsson (1959b), indicative of unimportant breed x management (group *vs* individual feeding) interactions. The results, though variable, indicate that it is necessary to be particular about interactions with these various management conditions in designing experiments on swine production.

Genotype x sex effects on carcass traits have also received some attention. No significant sire x effects were seen for any of the carcass traits by Kristjansson (1957). The same results were observed by Bouland and Berg (1959) on line x sex and by Hale and Coey (1963) on litter x sex interactions. Plank and Berg (1963) observed significant sire x sex effects on area of loin and total R.O.P. score among the several carcass traits they studied. Estimates of genetic correlations between the sexes (r_g) made by Smith and Ross (1965) were significantly different from unity in the case of average backfat thickness, firmness of fat score, carcass length, loin length, leg length, carcass depth, and length and area of eye muscle, the estimates being 0.81, 0.69, 0.91, 0.70, 0.79, 0.56, 0.34, and 0.79 respectively, indicating significant sire x sex interactions for these traits. The estimates for several other carcass traits they studied were not significantly different from unity.

In the study of McGloughlin (1968) all of the r_g values for carcass grade, carcass length, and shoulder fat were close to unity, and thus indicated the non-significance of sire x sex interactions for these traits. However, Hale and Southwell (1967) observed varying sex differences in two breeds in lean cuts, length

of carcass, and backfat thickness. Significant sire x sex effects were noted for marbling score but were unimportant for backfat, loin eye area, and yield of lean cuts in the study of Omtvedt and Jesse (1968). Finally, interactions of breeds with sexes were found significant in percent lean cuts, average backfat, backfat-last rib, backfat-last lumbar, and percent loin but were not significant for other carcass traits in the study of Quijandria *et al.* (1969).

Thus, even with differential responses of genotypes to sex in carcass traits, the results are variable. One has to look for them carefully while evaluating the breeding values of animals based on data of any one sex.

Traits Related to Fertility in Females.—In a study involving two breeds (Poland China and Chester White) and two rations (full and restricted feeding), Zimmerman *et al.* (1960) found breed x season interactions to have significant effects on age at puberty. The breed x feed level interactions were not significant in the same trait, although trial x breed x feed level interactions were found to be important. The latter observation was probably because of confounding of season effects with those of trials. In the experiment by Robertson *et al.* (1951) with gilts, both on pasture and in dry lots, Chester Whites were 11 days older than the Poland Chinas in the pasture lots ($P \leq 0.01$) and 1 day younger in the dry lots, indicating the presence of a breed x management interaction. In view of the results of these reports, further research on this question is suggested.

Semen Quality.—Lee (1961) collected semen in three fractions from 7 boars of 5 breeds (Poland China, Chester White, Berkshire, Duroc, and Hampshire) and recorded the total volume, volume of liquid portion, volume of gelatinous portion, sperm concentration, methylene blue reduction time, percent abnormal sperm, and percent of live and dead spermatozoa. Boar x fraction interactions were significant for all these variates.

Dogs

Freedman (1958) compared the behavioral response of four breeds of dogs (Shetland Sheepdog, Basenji, Wire-Haired Fox Terrier and Beagle) to "indulgent" and "disciplinary" modes of rearing. The presence of a breed x method of rearing interaction on the obedience of the animals at maturity was observed.

The strain selected on a restricted diet retained its selection advantage when it was placed on a full feed. The strain selected on full feed, on the other hand did not retain its advantage when placed on limited feed.

Rats and Mice

Laboratory animals are kept under more effectively controlled environmental conditions than farm animals, so the different kinds of genotype x environment interactions and their magnitude are likely to be less in them. Consequent to the same reasoning, results of breeding experiments in lab animals are not likely to hold true in the breeding of farm animals. However, some genetic experiments on lab animals, especially mice, have often given a clue to important animal

breeding principles. The contention of Falconer (1952) that the performance of a genotype in two separate environments should be treated as two different traits and the problem be dealt with as of a genetic correlation, was the key to open research on the importance of genotype x environment interactions.

Body Weights, Organ Weights and Body Measurements.—Falconer and Latyszewski (1952) reported the results of a selection experiment in support of Falconer's (1952) contention. They selected two strains of mice (from the same foundation stock) for 6-week body weight, one under *ad lib.* and another under restricted feeding conditions. Although there was an increase in body weight in both groups, the average increase per generation was greater in the full-fed strain and the heritability was larger under restricted feeding. However, an exchange of environments between the two strains was the critical test in revealing the importance of interactions. The strain selected under restricted diet was superior to the full fed strain when on limited feed. The fact that the latter showed no improvement over the former did not support Hammond's (1947) suggestions. However, under full feeding the full diet strain was superior, but the restricted diet strain did not fall short of it and showed a marked improvement over the unselected level for full diet. Moreover, the fat content of full fed mice was greater than that of the restricted fed, when both were reared under full feeding. Thus, the effects of selection under low plane were carried to the high plane but the reverse was not true.

These results, although they prove beyond doubt that selection of genotypes should be in the environment in which the animals are destined to live, were not in complete agreement with the theoretical expectations. To confirm this unexpected result, a more adequate experiment was conducted (Falconer, 1960). However, this time selection was for both high and low body weights, duplicated in normal and restricted (obtained by diluting the normal diet with indigestible fibre) diets. An exchange of diets was made between the two high lines and also between the two low lines. The results were similar to those of the previous experiment. Selections in both high and low planes were effective for growth in high plane but growth on a low plane was effective only by selection in a low plane. A "mirror image" of these results was obtained from selection for reduced growth on both planes of nutrition. Selection in both high and low planes was effective for reduced growth in a low plane, whereas, only selection in a high plane was effective for reduction in growth in a high plane. Thus, as pointed out by the author, the best "all-around" performance for higher growth rate was produced by selection in a low plane and that for reduced growth, in a high plane.

These results proved beyond doubt that animals should be selected in an environment in which they are destined to live. However, if it becomes necessary to select only in one of the environments, the one that is least favorable for the expression of the trait is to be chosen. It may be noted that heritability was

higher in a low plane (0.29, 0.20) in the study of Falconer and Latyszewski (1952). On the contrary, as was noted from a review of findings in dairy cattle, the heritability was higher in herds with better feeding and management with no change in the ranks and so selection in the better herds was suggested. Therefore, one has to study each case carefully before making final recommendations.

Another study similar to that of Falconer and Latyszewski (1952) was reported by Korkman (1961). However, Korkman's low plane was very low and thus the response to selection, though significant in a high plane, was not in the low plane. On exchange of the planes of nutrition, each strain was better than the other in the diet in which it was selected and the heritability estimate was higher in a high plane (0.218, 0.066). These differences in the findings from those of Falconer and Latyszewski (1952) were probably due to differences in the magnitude of the feeding levels they used. This may be the reason why it is necessary to determine the "optimum" environment in each case. Nevertheless, the conclusion in either of the studies was to select the animals in the environment in which they are to perform. Dalton and Bywater (1963) reported a similar experiment but they selected for total litter weight at weaning rather than individual weights. However, there was no significant selection response in either of the dietary regimes, nor was there any correlated response on dietary switch. The results were expected, however, because of the low heritability of the trait and the strong maternal influence, including milk production.

Thus, from all these selection experiments, the same conclusion is derived: "Select animals in the environment in which they are to perform."

In addition to the selection experiments under different diets described previously, other studies on interactions in body weights involving available genotypes and various diets have been reported.

Young (1952) compared three strains of mice on two different diets (cereal cake *vs* crushed oats) and two temperatures (20°C *vs* a hot temperature during winter). The slower growth rate of the C57 strain on crushed oats than the CBA strain suggested the presence of a strain x diet interaction.

The selection of two strains of rats, one on a standard and another on a roughage diet by Kidwell *et al.* (1960) showed significant strain x nutritional regime effects for 70-day body weight and several body measurements among the females; but, except for the proportion of small intestine to body weight, none of them were significant in the male.

Sire x nature of protein (a standard 20% crude protein diet *vs* a diet containing 14% vegetable protein) interactions for litter weight at 15 days after birth were found nonsignificant by Bakels (1963) from a comparison of four sire progeny groups of mice, each with 334 daughters, although Bakels pointed out that the number and size of significant differences in litter weight between sire groups were not the same in the two diets.

Recently, Bailey *et al.* (1970) compared the effectiveness of selection on two diets (a commercial diet fed *ad libitum* and a low plane diet, also fed *ad libitum*) with two inbred lines of rats and a random control in each group. After selection for six generations, top gaining, select line sires were mated with control dams on both diets to study the importance of sire line x nutrition regimen interactions. Realized heritability estimates for postweaning gain were 0.38 ± 0.11 and 0.32 ± 0.09 for regular diet select lines and 0.17 ± 0.10 and 0.28 ± 0.10 for low plane diet select lines. These figures indicate that selection should be more effective in a regular diet as compared to a low plane diet. The sire x progeny diet/sire line interactions were significant for 28-day weight, postweaning gain, and 70-day weight in both males and females, although the sire line x diet interactions were not important for any of those traits. These results present a situation where the interactions involving intra-population genotypes and macro-environments (Type B of McBride, 1958) were more important than those with interpopulation (different inbred lines) genotypes and macro-environments (Type D of McBride, 1958). The results of all these studies on interactions with nutritional differences, although variable, do produce evidence for their possible existence in such experiments.

Interactions of genotypes with sex of the animals have reached attention in mice as well. Korkman (1957) selected two lines of mice, one for maximum size (largest male and smallest female in a litter) and another for minimum size (smallest male and largest female in a litter) sexual dimorphism in body weight at 90 days of age. Selection was effective for increased sex difference, as it raised from 2.2 to 4.3g., whereas, there was no response to selection in the other group. Thus, the differential response of the genotypes to sex was demonstrated. Rahnefeld *et al.* (1963) reported that the genetic correlation for growth between the sexes was less than perfect and the average heritability estimates were 0.243 ± 0.074 and 0.264 ± 0.078 for ♂♂ and ♀♀, respectively. One of the most interesting papers on the interaction of genotypes and sexes was by Eisen and Legates (1966). Their theoretical considerations on the biometrical relationship among genetic variance of sexual dimorphism, genotype-sex interaction and genetic correlation between the sexes for a quantitative trait have been reviewed earlier. Further, from analyses of the data on 3-, 6- and 8-week body weights of 781 ♂♂ and 767 ♀♀ progeny in three generations of random bred ICR albino mice, they reported heritability estimates for three-weeks, six-weeks, gain from three-weeks to six-weeks, and eight-week weights to be .010, .084, .240 and .142, respectively. The genetic variances of the differences between males and females were significant for only postweaning gain and eight-week weight and the corrected estimates of interaction components were also relatively large for the same traits. The corresponding corrected genetic correlations in their study were 0.640 ± 4.095 , 0.903 ± 0.066 , 0.680 ± 0.195 , and 0.796 ± 0.132 , respectively. All these estimates indicate a possible genotype x sex interaction for postweaning growth and eight-week body weight but not for 3-week and 6-week weights.

Significant differential responses of strains by sexes were also observed by Marshall *et al.* (1969) for body weight, body fat, tibia length, and leg skinfold but not for body length, tail length and girth on comparison of three strains of rats. However, they found the strain x age interactions to be significant for most of the traits.

Relative adrenal weights in mice were also influenced by dam x sex, dam x laterality, sire x sex, and sire x laterality interactions in tests by Meckler and Collins (1965) with four inbred strains and all possible crosses among them. Complementary to their results, Spickett *et al.* (1965) also reported a significant strain x sex interaction on relative adrenal weight.

The findings of all these studies present enough evidence for the presence of genotype x sex interactions on body weights, organ weights, and body measurements to take these into consideration in breeding experiments.

Cockrem (1963), on comparing the adaptability of two strains (one of high body weight and short tail length and another of low body weight and long tail length) at temperatures of 7°C, 21°C (control) and 32°C, observed no differential response of the strains to the three environments on body weight at six weeks of age, although such a differential response was present for tail length. However, Harrison (1963) found two inbred strains to react differently on testing in a hot environment of 32°C with respect to body weight. Added to this evidence, Barnett (1965) concluded from reviewing his extensive work that adaptation of inbred strains of mice to -3°C was different from that to normal 21°C. Although the reports are few, the results indicate the existence of interactions with environmental temperatures affecting growth in mice.

Finally, Hull (1963) found sire x environment (not specified) interactions were larger with sires from F₂ cross of inbred lines than when they were F₁s for tail length (a trait with higher h²); no such difference was observed for body weight (a trait with lower h²). These results indicate the importance of interactions with larger differences in the genotypes.

Feed Consumption and Feed Efficiency.—Timon and Eisen (1970) observed significant line x feeding level interactions in feed consumption but not for feed efficiency in comparing two lines of mice (a high line selected for increased postweaning gain and a control line) in two feeding levels (*ad libitum* vs restricted feeding). In the same experiment, they also observed significant line x sex interactions for feed consumption as well as feed efficiency. However, sire line x nutrition regimen interactions were found to be negligible by Bailey *et al.* (1970) and no significant line x sex effects were noted in rats for feed intake and feed efficiency in the study of Abdel-Malek (1966). In view of the variable results of these few studies, further research on interaction effects on these traits is suggested.

Reproductive Traits.—Young (1953) observed a differential response of different strains to the type of diet in litter size. The RIII strain with the smallest

litter size showed no change for this trait on switching from cake to oats, whereas the other two strains showed considerable reduction. In total fertility (number of offspring produced by each ♀ ♀ under 20 wks. of age), the C57 strain produced relatively fewer offspring when fed oats compared with cake than the other two strains. However, no sire group x diet interactions for litter size were noted by Bakeis (1963) and the response to dietary switch on litter size was observed to be small or negligible in the study of Dalton and Bywater (1963). The lack of consistency in these results calls for further research to arrive at any broad conclusion on the importance of the interaction effects on the reproductive traits.

Blood Glucose and Liver Glycogen.—In comparing the physiological responses of three inbred lines of mice (two of them were insulin tolerant) to three levels of insulin dosage (0, ½ and 50 units), Chase and Kidwell (1965) noted significant line x dose, line x sex, and line x sex x dose interactions for blood glucose but none of the interactions were significant for liver glycogen. The results suggest a genetic basis for insulin tolerance different from that for blood glucose.

Tolerance to Sodium Chloride.—McNutt and Dill (1963) reared two strains of mice (a resistant and a susceptible strain) and various crosses and backcrosses of these in 4 percent NaCl solution as the only source of drinking water. The mortality reached 50 percent at one week of age in the susceptible strain as compared to 35 weeks in the resistant strain. This figure varied among F₁, F₂, and F₃ populations. This is an example where the importance of interaction in extremes of environmental differences is illustrated.

Behavior.—A differential response of three strains of mice to maternal injection of adrenalin during pregnancy in the activity of the offspring was observed by Thompson and Olian (1961). The offspring from low-activity females were more active than those of control females of the same strain, whereas the activity was lowered in the offspring of medium-activity females as compared to those in the control group. Further evidence of the differences in the response of offspring from females with different levels of activity to maternal injection of adrenalin in rats was reported by Thompson *et al.* (1962). In view of these findings, one should be cautious in making generalized statements on the action of such hormones. It would be interesting to see if groups of genotypes in marker animals would respond differently to treatments of different levels of drugs and hormones for health and production. A similar study with different kinds of stress was reported by Weir and DeFries (1964). They exposed half the ♀ ♀ of each of their two strains to three types of stress (swim tank, tilt box, and brightly lighted open field) after being paired with ♂ ♂ of their own strain at 49 days of age. On testing the offspring at 40 days of age for open field behavior, highly significant strain x treatment and strain x sex interactions were noted. Complementary to these findings are the results reported by Meier (1964). He observed highly significant strain x sex, strain x age, and strain x sex x age interactions on the maze performance in six strains of mice. Finally, Bronson

(1963) observed differential endocrine responses of the species of mice (C57 and deer mice) when the adult males were first caged one, two, four, or eight per cage for one week, exposed to trained fighters for 15 min./day for seven days and subsequently kept with strange males. The relative adrenal weight increased at higher densities in C57 but no such change with density was noted in the deer mice. Based on these results, it would be interesting to know if differences in the endocrine responses of similar genotypes exist in herds of different sizes in case of farm animals or even among members of human families residing in big cities and small communities.

Poultry

Domestic Fowl: Because of the confined system of housing, it has become possible to control the environmental factors more effectively in raising the domestic fowl than in other species of farm animals. However, there are certain problems peculiar to birds alone. The embryos develop inside the eggs, outside the body of the hen, and thus, are exposed to external environmental conditions, such as temperature; humidity; management and make of the incubators; and date of hatch. Moreover, the necessity for large-scale production has turned poultry farming to poultry industry, leading to specialization on different aspects of poultry production. Consequently, the birds are produced in the breeder's flocks and used in the commercial flocks widely distributed over regions for their performance. Although domestic fowls are well known for their adaptedness as demonstrated by the performance of certain breeds in almost every country of the world, they pose a different problem in countries such as the U.S.A., Canada, Great Britain, and Australia where much progress has already been made in the breeding of these birds. Because of high fertility and a short generation interval, much of the additive genetic variance has been exhausted and many strains have been developed within each of the selected breeds. Many types of hybrid poultry are produced for commercial use, especially in the U.S.A. Domestic fowl are known by the name of the hybrids rather than by breeds, and above all, the poultry business has become the most competitive.

In view of the aforesaid reasons, it has become necessary to run random sample tests on strains used within a region and recommend as a routine measure, the type of strain or hybrid for maximum production in that location. However, realizing the possible influence of the genotype x location interactions on the evaluation of the strains in random sample testing, some of the states in the U.S. have introduced the practice of testing all strains at each of the locations with a view to recommending the appropriate strain for a particular farm or evaluating the general performance ability of the strains in that region. This has, at many places, enabled the commercial producer to survive the competitive market. In view of what has been said, it may be easily seen why there are more reports on interactions involving locations than any of the several environmental

factors. Also, studies on interactions have been made more extensively in domestic fowl than in any other species of farm animal. An attempt will be made to review the reports as briefly as possible, especially since some of them have been reviewed by McBride (1958).

Egg Production: Although, in reality, "egg production" is a compound character, it is used here to refer to the "number of eggs laid in a specified time" to be in concordance with its common usage. As stated earlier, there have been more studies on interactions dealing with locations than any other environmental effects. The word "location," as used here, includes farm locations of varying geographical separation. These studies, as expected, presented variable results.

Genotype x location interactions of important magnitude have been observed by some, necessitating their consideration in the poultry breeding plans (Nordskog and Arvidson, 1948; Wilson, 1949; Nordskog and Kempthorne, 1960; Abplanalp and Menzi, 1961; Abplanalp *et al.*, 1962; Bowman and Powell, 1964; Cook *et al.*, 1963; Beck and Baker, 1964; Krause *et al.*, 1965; Nordskog, 1966; Marks *et al.*, 1969c). However, such interaction effects were not found to be significant by others (Gowe, 1952; Gowe and Wakely, 1954; Weber and Le Roy, 1956; Hill and Nordskog, 1956; Yamada and Ito, 1959; Yamada, 1960; Becker, 1961; Abplanalp and Marrou, 1961; Hull and Gowe, 1962; Van Vleck *et al.*, 1963; Hull *et al.*, 1963; Tindell *et al.*, 1967b; Marks *et al.*, 1969a). Added to these conflicting results, a location x dam's breeding but not a location x B-locus (a blood group system) interaction effect was observed by Allen (1962). The variable results suggest a prior testing of all the available strains at each of the locations for their commercial use. In view of the extensive studies already made, it was decided not to describe the genotypes and locations for each of the studies. However, the interesting parameters estimated in a few of the studies are shown in Table 16 to emphasize the relationship of these estimates to the importance of genotype x location interactions. The inverse relationship of the r_g values with significance of interactions may be specially noted. Added to these estimates, the genetic bias (previously explained) for hen-day production from first egg and hen-housed production were estimated to be 0.18 and 0.31, respectively, by Dickerson (1960) from a comparison of several matings in 12-13 locations. Such an estimate was found to be 0.23 for hen-day production by Beck and Baker (1964) for interactions of several varieties and locations. These low estimates indicate the magnitude and importance of interactions with location effects.

Interactions of genotypes with year effects have been found important in some of the studies (Hill and Nordskog, 1956; Tindell, 1961; Harms *et al.*, 1967; Wilson *et al.*, 1967), whereas these were estimated to be nonsignificant by others (Abplanalp and Marrou, 1961; Abplanalp *et al.*, 1962; Tindell *et al.*, 1967b; Marks *et al.*, 1969a). The results are again variable. Therefore, selection of strains based on test performance for more than one year should be more dependable than from one year alone. Besides these evidences, Wilson (1949) observed a

significant breed x month interaction, the months reflecting the effects of temperature at California, Oklahoma, and Western New York.

Because feed is one of the most important constituents among the various environmental factors, studies on its interaction with the genotypes have always received much attention. A strain x feed level interaction with significant effects on egg production was observed by Proudfoot and Gowe (1967). Such an effect, however, was found to be significant but of low magnitude only in one of the four years in the study of Gowe *et al.* (1962). On the other hand, genotype x feed level effects were found to be nonsignificant by others (Schneider *et al.*, 1955; Hull *et al.*, 1963; Hull and Gowe, 1962). The results of these reports, though few, indicate no differences in the response of the genotypes to various feeding levels.

An interesting study on the differential response of the genotypes to starvation has been made by Abplanalp (1962). He exposed selected (selected for 31 years) and unselected lines to different weekly periods of starvation and found that the difference in average egg production between 33- and 48-hour treatments was larger in unselected lines than in the selected ones, indicating the existence of genotype-environment interactions.

Fox *et al.* (1960), in a comparison of two types of laying birds fed two rations differing in energy levels, observed a highly significant breed x ration interaction. However, no strain x energy level interaction was noted in the study of Kondra and Sell (1966). In another study (Kondra *et al.*, 1968), three egg producing strains responded differently to three rations differing in the amount and source of added fat.

Studies on the responses of different genotypes to rations differing in their protein levels have generally indicated important interaction effects (Harms and Waldroup, 1962; Deaton and Quisenberry, 1965; Harms *et al.*, 1966). Results complementary to these were also observed by Harms *et al.* (1967) from a comparison of two strains of pullets in diets differing in the methionine level. However, Kondra and Sell (1966) and Marks *et al.* (1969a) found no such differential response to diets of varying protein levels.

Studies on interactions involving housing systems have received considerable attention in the domestic fowl. French and Ledger (1954) noted differences in the responses of three breeds (Cambars, Legbars, and Welsummers) to three different systems of housing: (1) deep litter, (2) grass runs with deep litter houses, and (3) grass runs with bare-floored houses. On the other hand, breed group x floor type (slatted *vs.* wood-shavings litter) interactions were found to be nonsignificant by Yao (1959). Another rearing method used for the comparison of six different Leghorn strains was confinement *vs.* range, where no significant interaction effect for survivor egg production in one year was observed by Proudfoot and Gowe (1961).

TABLE 16

Genotypes	Locations	Measure of egg production	Estimated parameters		Significance of interaction	Author(s)
			r _g	% interaction component		
19 different hybrid combinations	4 widely separated testing locations	Av. annual	0.55	43.0	Important	Nordskog and Arvidson (1948)
Several varieties of laying chickens	Locations in England and Wales	Hen-month production	0.72	39.7	Sig.	Bowman and Powell (1964)
		Hen-housed production	0.76	32.9	Sig.	
8th and 9th tests by Swiss poultry breeding cooperative	6-12 farms	500-day test period	0.74	----	Sig.	Abplanalp and Menzi (1961)
23 repeat entries in California Random Sample egg laying tests. (1956 and 1957)	10 and 9 commercial farms respectively	22-33 wks. 1956-57	0.58	1.9	Of relative importance as the genetic components were also small	Abplanalp <i>et al.</i> (1962)
		1957-58	0.62	2.0		
		39-58 wks. 1956-57	0.00	5.2	Of relative importance as the genetic components were also small	
		1957-58	0.34	2.4		
		59-78 wks. 1956-57	0.17	4.6	Of relative importance as the genetic components were also small	
		1957-58	0.50	1.9		
22-78 wks. 1956-57	0.06	5.7	Of relative importance as the genetic components were also small			
1957-58	0.54	2.0				
Sires of 2 strains of W.L. birds in Canada	3 branch farms of research branch, Canada	Hen-housed	St1 0.85	---	NS	Hull and Gowe (1962)
			St2 0.77	---	NS	
		Of survivors to 500 days	St1 0.97	---	NS	
			St2 0.93	---	NS	

Sig. = Significant; NS = Not significant.

Comparisons of genotypes in cages *vs.* floor pens have shown varying responses. These interaction effects were found significant by Baily *et al.* (1959) and Lowry and Abplanalp (1970). In the study of Gowe (1956), such an interaction effect was significant for survivor's egg production but not for hen-housed egg production. Likewise, breed x system of housing as well as interactions involving sires and dams in Brown Leghorns were nonsignificant, but the latter types were important in the Light Sussex birds studied by Hale (1961).

Complementary to these findings were those of Onishi and Miyazono (1962), where mating system (inbreds *vs.* incrosses) x housing system (battery *vs.* laying pens) interaction effects were nonsignificant, whereas stock x housing system effects among inbreds but not incrosses were observed to be significant. At the other end, interactions with cage *vs.* pen floors were found unimportant in the studies of Lowry *et al.* (1956) and McBride (1962), although in the latter study, the heritability estimates for egg number in the three environments, cages, semi-intensive, and intensive housing, were 0.18, 0.00, and 0.55, respectively.

Studies dealing with different cage densities have generally indicated important interaction effects (Cook and Dembnicki, 1966; Wilson *et al.*, 1967; Fowler and Quisenberry, 1969). However, an interaction effect of this kind was found to be nonsignificant by Adams and Jackson (1968).

Finally, comparisons of housing systems were with birds of different genetic background kept intermingled or in separate pens. Interactions with these effects were found to be important by some (Morley and Smith, 1954; King and Bray, 1959), but nonsignificant by others (Jaap, 1954; Proudfoot *et al.*, 1957).

Results of all these studies dealing with some kind of housing system, though variable, do indicate their existence and suggest their consideration in selecting strains for any given farm.

Responses of various genotypes to different dates of hatch were found to vary significantly by Yamada (1959) and Yamada (1960). However, such a differential response was found to be of low magnitude (4%) by Abplanalp (1956). More studies on the importance of interactions involving hatch effects for egg production are needed to arrive at any broad conclusion.

Long *et al.* (1966), in their observation on the performance of four strains of White Leghorns (one strain in each year) in seven different combinations of ventilation rates and temperature, found significant strain x environment (reported as year x environment) interaction effects (but nonsignificant if treatment 5 excluded) on hen-day production.

Finally, a significant strain (5 commercial strains) x light regime interaction effect on egg production was noted by Proudfoot and Gowe (1967). Further investigations will prove the importance of this finding.

Egg Weight: Many investigators testing birds of varying genetic background at different locations have found significant interaction effects (Johnson and Gowe, 1956; Nordskog and Kempthorne, 1960; Becker, 1961; Bowman and

Powell, 1964; Beck and Baker, 1964; Nordskog, 1966; Marks *et al.*, 1969c). However, these genotype x location effects were not found to be important by others (Abplanalp *et al.*, 1962; Allen, 1962; Van Vleck *et al.*, 1963; Tindell *et al.*, 1967b; Marks *et al.*, 1969a). The genetic bias figures for eight-month egg weight estimated by Beck and Baker (1964) and Dickerson (1960) were 0.58 and 0.09, respectively. It may be noted that traits described as "egg size" were also included under egg weight, and locations, as a matter of fact, include not only differences in their geographical locations, but also the management and other practices peculiar to the farms. Although a few of the aforesaid reports indicated interaction effects were unimportant, the results of others indicated their importance on egg weight.

Stock x year interaction effects were reported significant by Tindell *et al.* (1967b) and Marks *et al.* (1969a), whereas an interaction of this kind was not found important by Abplanalp *et al.* (1962). Redman and Shoffner (1961) found no significant cross (polyallelic) x season interactions. However, a line x month interaction was noted by Marion *et al.* (1964). Probably, more studies are needed to draw any inference of a general nature about the importance of these effects.

Interaction effects involving different levels of feeding have generally been found unimportant (Hull and Gowe, 1962; Gowe *et al.*, 1962; Hull *et al.*, 1963).

A strain x dietary energy level interaction was found to have significant effects on egg weight by Kondra and Sell (1966). However, Kondra *et al.* (1968) found no significant influence of strain by source and level of fat in the diet interactions for the same trait.

The effects of different levels of protein in the rations were found to interact significantly with the different genotypes in the studies by Moreng *et al.* (1964) and Deaton and Quisenberry (1965). Harms *et al.* (1967) noted a significant breed x methionine level interaction effect. However, such interaction effects were found to be unimportant by others (Harms *et al.*, 1966; and Marks *et al.*, 1969a).

From the review of these reports dealing with nutritional differences, it appears that interactions with differences in quality but not of quantity are important, requiring their consideration in poultry breeding.

Studies of interactions dealing with housing and rearing methods such as slatted *vs.* litter floor and confinement *vs.* range rearing were found to have no significant effects on egg weights by Yao (1959) and Proudfoot and Gowe (1961), respectively. More studies of this nature are needed.

A differential response of genotypes to cage *vs.* floor housing system was observed by Bailey *et al.* (1959), but varying results on interaction effects of this kind were noted by Hale (1961) and McBride (1962). In the former study, no interactions were noted involving breeds or sires within breeds but dams within each of the breeds during one of the three years showed interactions. In the latter report, interactions involving cage *vs.* intensive housing were observed but

not for cage *vs.* semi-intensive or semi-intensive *vs.* intensive housing. Also, the heritability estimates reported by McBride (1962) were 0.68, 0.50, and 0.64, respectively, for cage, semi-intensive, and intensive housing. On the other hand, these interactions were found to be nonsignificant by others (Gowe, 1956; Lowry *et al.*, 1956; Lowry and Abplanalp, 1970).

Cage density effects on egg weight varied significantly among different genotypes in some of the studies (Cook and Dembnicki, 1966; Wilson *et al.*, 1967). However, no such differential responses were observed by Adams and Jackson (1968).

Finally, no differences in the responses of strains to housing, separately or when they were intermingled, were found by King and Bray (1959).

The review of these reports dealing with rearing and housing methods on the whole do not indicate the interaction effects to be of any significance.

Interactions dealing with date of hatch effects were observed to be nonsignificant in the studies by Abplanalp (1956) and Allen (1962).

Differences in temperature were seen to affect various genotypes differently by Huston *et al.* (1957) and Clark and Amin (1965).

Strain x light treatment interactions, as observed by McClary (1960), were of no significance.

No line x age of hen interaction effect was found in the investigation by Marion *et al.* (1966).

A final reference on egg weight was the report of Kliesch and Horst (1966), who observed significant strain x management interaction effects. The genetic correlation for hens of the same strain in different environments was estimated to be 0.66.

Further investigations on interactions involving dates of hatch, temperature, light, and age of hen effects are suggested.

Age at Sexual Maturity. The method of determining the age at sexual maturity varies among different experiments. Usually, it is expressed as the age at which the first egg is laid. However, others (for example, Nordskog and Kempthorne, 1960, and Nordskog, 1966) expressed this trait as the age at 50 percent production. All of these, as well as the various genotypes reported in the references are grouped together in the following review.

Interactions involving birds of varying genetic background and different locations were observed to have significant effects on the age at sexual maturity by some (Nordskog and Kempthorne, 1960; Cook *et al.*, 1963; Nordskog, 1966; Krause *et al.*, 1965; Marks *et al.*, 1969c), whereas others found them unimportant (Yamada and Ito, 1959; Abplanalp *et al.*, 1962; Hull and Gowe 1962; Hull *et al.*, 1963; Van Vleck *et al.*, 1963; Marks *et al.*, 1969a). Complementary to the latter findings was a study by Dickerson (1960), indicating the genetic bias to be 0.33; also complementary are the estimates of r_g of 0.93 and 1.05, respectively, in strains 1 and 2, reported by Hull and Gowe (1962). The reviewed results, al-

though conflicting, do indicate the possibility of the existence of important genotype by location interaction effects on the age at sexual maturity and so these need to be considered in the selection of stocks for any given farm.

In the studies dealing with year effects, interactions were found to be non-significant by Abplanalp *et al.* (1962) and Marks *et al.* (1969a), although Tindell (1961) noted their presence. Further investigations are needed to arrive at any general conclusion.

The effects of different feeding levels were observed to interact significantly with the respective genotypes in the studies of Gowe *et al.* (1962) (but of low magnitude), Hull and Gowe (1962) and Hull *et al.* (1963). The reports, though few, do indicate their importance in the poultry breeding plans.

In the studies dealing with comparisons of cages *vs.* floor pens, the interaction effects were generally unimportant (Gowe, 1956; Lowry *et al.*, 1956; Lowry and Abplanalp, 1970). Hale (1961), although he observed no interactions involving sires or dams within Light Sussex, found those involving dams (but not sires) of Brown Leghorn to be important. Thus, the unimportance of the interaction effect was almost consistent in these few reports reviewed. The findings were also complementary when King and Bray (1959) compared 10 strains of each of three breeds housed separately with those intermingled.

Investigations of interactions with date of hatch effects have shown variable results. Osborne (1951) observed significant interactions associated with change in ranking of the family means, whereas these were found to be unimportant by others (Abplanalp, 1956; Yamada, 1959; 1960). In the study of Skaller and Sheldon (1955), interactions were significant in two of the four flocks and Greenwood and Blyth (1946) observed a differential response of sires to season of hatching. The results of these studies indicate the possibility of the presence of differential responses to dates of hatching on age at sexual maturity of pullets.

The heritability estimates for age at sexual maturity under three lighting regimes, no artificial lighting, restricted lighting, and 14-hr. day length, reported by Osborne (1954) were 0.48, 0.56, and 0.39, respectively, indicating the presence of an interaction. These findings were also supported by the observation of a significant strain x light regime interaction by Bowman *et al.* (1964). However, an interaction of this kind was found nonsignificant by McClary (1960). In view of the small number of reports, further studies are needed to determine the importance of this effect.

Fertility and Hatchability: From the economic standpoint, fertility and hatchability are important traits for poultry breeders. Any differential response of the genotypes to the various environmental factors would affect the cost of chick production.

The heritability estimates for fertility and hatchability in five hatching seasons were noted by Gilbreath *et al.* (1962) to be different, indicating the presence of a sire x hatch interaction. However, Allen (1962) observed no hatch x dam's

breeding or hatch x B-locus (a blood group system) interaction effects except for the latter type on percent hatch of fertile eggs. Significant mating plan x hatch effects (but not mating plan x age of egg) interactions were found by Lax (1964). Differential responses of two types of birds to four storage periods as well as to the use of Cryosac bags were noted by Bowman (1969). Finally, Davis (1955), on comparing hatchability of eggs from New Hampshire hens incubated at normal atmospheric air and at normal air supplemented with 25 percent oxygen, found no significant hen x oxygen environment interaction effects on this trait. From these reports, it may be seen that extensive studies on interactions for fertility and hatchability have not been made. Further studies on these aspects at the breeders' flocks are suggested.

Semen Quality: Weber and Lortscher (1954) observed a differential response of W.L. cocks of different origin to varying ambient temperatures on their fertility. A similar study by Clark and Sarakoon (1967) indicated differences in semen volume and sperm concentration of four strains of W.L. cocks in different ambient temperatures. However, no such difference was observed for the methylene blue reduction time. The reports are too few to draw any inference. For economic reasons no studies specifically for interaction effects on semen quality are suggested. However, analysis of data if available from other studies would be helpful in revealing the importance of these interactions.

Mortality and Viability: In any successful farm animal business, the animals have to live to perform. Thus, the economic importance of these traits cannot be over emphasized. The method of evaluation varies considerably among the studies, some measure the percent mortality and others measure it in terms of viability. Moreover, the age at which these figures are calculated varies greatly. As the age at death is important in different aspects of the poultry business, attempts are made in the following review to describe the type of mortality within parentheses following each reference.

Genotype x location interactions were found to have significant effects in the following studies: Hill and Nordskog (1956) (hen-housed); Dickerson, (1960) (0-20 wk. and 21-72 wk., genetic bias being 0.76 and 0.61, respectively); Nordskog and Kempthorne (1960) (adult); Abplanalp and Menzi (1961) (viability to 500 days, $r_g = 0.26$); Beck and Baker (1964) (laying house livability, genetic bias being 0.41); Bowman and Powell (1964) (rearing and laying, r_g being 0.49 and 0.50, respectively); Nordskog (1966) (adult, 14.8% of total variance); and Marks *et al.* (1969c) (rearing and laying). Varying results were noted by others: Allen (1962) (% survival from hatching to 160 days and from 160 to 500 days; location x B-locus genes—not significant for either trait but location x dam's breeding—significant for the latter); Marks *et al.* (1969b) (significant for 0-8 wk. but not for 1-8 wk.); and Tindell *et al.* (1968a) (0-8 wk. and 1-8 wk., parent stock x growing location—not significant for either but parent stock x parent location—significant for the former). However, these interaction effects

were found to be unimportant by others: Gowe and Wakely (1954) (rearing and laying); Abplanalp and Marrou (1961) (8-78 wks.); Becker (1961) (laying house); Abplanalp *et al.* (1962) (brooder house); Tindell *et al.* (1967b) (rearing); Tindell *et al.* (1968b) (0-8 wk. and 1-8 wk.); and Marks *et al.* (1969a) (rearing and laying). Thus, while the results were not consistent, they presented enough evidence indicating the possibility of the existence of genotype x location interactions.

Interactions involving year effects were seen to be significant for hen-housed mortality by Hill and Nordskog (1956). Tindell *et al.* (1968b) observed these effects to be significant for zero to eight weeks but not for one to eight weeks mortality and in the study of Marks *et al.* (1969a), they were important for rearing but not for laying mortality. However, these interactions were of no significance in the studies by Abplanalp and Marrou (1961) (8-78 wks.); Abplanalp *et al.* (1962) (brooder house); Tindell *et al.* (1967b) (rearing); and Tindell *et al.* (1968a) (0-8 wk. and 1-8 wk.). As the reports are few and the results are inconsistent, further investigations on this line are suggested.

Studies of interactions dealing with different feeding levels were found to have significant effects on laying house mortality by Proudfoot and Gowe (1967), whereas these were observed to be unimportant by Gowe *et al.* (1962) (147-500 days) and Hull *et al.* (1963) (laying house).

The interaction effects involving different protein levels in rations were found nonsignificant by Marks *et al.* (1969a) (rearing and laying) and Marks *et al.* (1969b) (0-8 wk. and 1-8 wk.). A significant breed x phosphorus level interaction was observed by Gardiner (1969) on percent livability to four weeks of age. Although the results of all these studies dealing with differences in both quantity and quality of the ration were generally unimportant, more studies are needed to arrive at any conclusion.

Interaction Effects Involving Differences in Housing Systems: The following reported reports were noted on these influences: Nonsignificant for laying house mortality with cage *vs.* floor (Gowe, 1956); unimportant for laying house mortality when kept in separate pens or intermingled (King and Bray, 1959); no evidence of interaction for laying house mortality in confinement *vs.* range (Proudfoot and Gowe, 1961); not significant for lay period mortality with different cage densities (Cook and Dembnicki, 1966; Adams and Jackson, 1968); unimportant for zero to eight weeks and one to eight weeks with two floor spaces (Tindell *et al.*, 1968b); and significant for livability to four weeks with two battery types (Gardiner, 1969). These evidences show that interaction effects involving differences in the housing systems are generally not important for mortality.

Finally, in a study involving five commercial egg production strains and four light regimes, Proudfoot and Gowe (1967) observed significant interaction effects on laying house mortality. More research along this line is needed to arrive at any conclusion.

Egg Quality Traits: The traits determining the quality of eggs are many. The egg weight, though the most important one of these, was considered separately because of its greater economic importance. The other traits have been grouped in various combinations among the several reports. Attempts will be made to mention them in groups but separately for each reference.

The results of the studies dealing with the genotype x location interaction effects include: nonsignificant for albumen height and Haugh units but significant for blood spot incidence, observed by Johnson and Gowe (1956); genetic bias of 0.08, 0.34 and 0.00, respectively, for albumen score, sp.gr. and egg shape, reported by Dickerson (1960); not significant for Haugh units (Nordskog and Kempthorne, 1960); important for shell thickness score but not for egg albumen score, observed by Nordskog (1966); 1.8 percent and 0.5 percent of total variance, respectively, for albumen score and shell strength score, estimated by Van Vleck *et al.* (1963); significant for sp.gr. and Haugh units but not for albumen height and percent defects (meat and blood spots) at 200 days of age and nonsignificant for all these traits at 350 days of age, reported by Tindell *et al.* (1967b); unimportant for sp.gr., albumen height, Haugh units, and incidence of meat and blood spots as found by Marks *et al.* (1969a); and significant interactions with parent locations for sp.gr., albumen height, and Haugh units, both at 200 and 350 days of age but with growing locations, significant only for percent defects at 350 days of age of all these traits and both ages, reported by Marks *et al.* (1969c). The results of these studies, although they vary greatly, indicate the possibility of the existence of genotype x location interactions on some of the egg quality traits.

Interactions with year effects were found by Tindell *et al.* (1967b) to be significant for sp.gr., albumen height, Haugh units, and percent defects at 200 days of age but not for any of these traits at 350 days of age. However, in the study of Marks *et al.* (1969a), these interactions were not significant for any of the traits at 200 days of age and they were found to be important only for albumen height at 350 days of age. The varied results of these few studies suggest further investigations are needed.

In a study dealing with season effects, Redman and Shoffner (1961) found no significant interaction effects on sp.gr., egg shell color, egg shape, egg weight, and Haugh units. Line x month interactions were also noted to be significant for percent shell but not for percent yolk or percent albumen in the study of Marion *et al.* (1964).

Kondra and Sell (1966), in their study on the comparison of commercial strains under different energy levels in the ration, observed significant interactions for thick albumen weight and percent, and thin albumen percent but not for shell thickness, weight and percent of yolk, twin albumen weight, and Haugh units.

For rations differing in levels of fat, Kondra *et al.* (1968) observed no significant interactions for average yolk weight, whereas such interaction effects were found to be important for several fatty acids in the yolk by Sell *et al.* (1968).

With diets of varying protein levels, Moreng *et al.* (1964) observed significant strain by ration interaction effects on Haugh units but they were not important for eggshell thickness. Similar important differential responses were observed for Haugh units and shell thickness by Deaton and Quisenberry (1965) but were nonsignificant for shell thickness, yolk weight and percent, thick albumen weight and percent, thin albumen weight and percent, and Haugh units in the study of Kondra and Sell (1966). The results of these studies, although not consistent, present evidence for the presence of interactions involving differences in the ration on the egg quality traits.

In a study dealing with housing of different strains in confinement *vs.* those provided with range, Proudfoot and Gowe (1961) found no significant interaction effects on albumen height, sp.gr., blood spots, and meat spots. Likewise, nonsignificant results were observed by Yao (1959) for blood spots and Haugh units (both fresh and 3-day old eggs) in his study involving slatted floor *vs.* litter floor. However, Adams and Skinner (1963) observed significant strain x type of house (differing in floor density, type of floor, and other aspects) interactions on Haugh unit values. On the other hand, in the studies dealing with a comparison of cage densities, no evidence of interactions was found for the incidence of blood and meat spots by Cook and Dembnicki (1966) and for the internal egg quality by Adams and Jackson (1968). These results indicated the unimportance of the interaction effects involving differences in the housing system.

In the studies dealing with storage of eggs, Proudfoot (1962) found significant interactions for decline in the interior egg quality on storage at 30°F after 16 weeks but not till 12 weeks and at 70°C, these were important at two and three weeks but not at four weeks. Strain by temperature (65 ± 5°F *vs.* 70-100°F) interaction effects were found to be important for Haugh units but not for shell thickness and percent shell by Clark and Amin (1965). Other studies dealing with the genotype by storage interactions showed no significant effects on the decline in egg quality (May *et al.*, 1957; Eisen *et al.*, 1963; Fry *et al.*, 1965). Added to these findings, McClary and Bearse (1956) reported r_g values of 0.94 and 0.99 for fresh and stored eggs at two different ages of the hens. However, high heritability estimates for change in egg quality during storage were reported by Kyle and Mitchell (1958). It may be pointed out that higher heritability estimates for differences between environments in a trait within each genetic class indicates larger interaction effects as previously described. As may be seen, the reports are few and the results are not consistent. Further studies may indicate the importance of such interaction effects.

Line by age of hen interaction effects were reported by Marion *et al.* (1966) to be significant for contents of moisture, lipids, fat-free solids and all fatty acids

except the myristic. Similar studies on interactions dealing with period (sampling done in different periods of a year) effects revealed the following results: significant for Haugh units (Grimes, 1954); a repeatability estimate of 0.77 for Haugh units of five consecutive trap nested eggs/bird (Dickerson and Lamoreux, 1954); and significant for egg yolk cholesterol (Collins *et al.*, 1968). Finally, the r_g values reported by Kliesch and Horst (1966) for traits of hens of the same strain in different management systems and different measurement times, were as follows: yolk weight, 0.62 and 0.74; albumen weight, 0.70 and 0.99; shell weight, 0.70 and 0.87; shell thickness, 0.82 and 0.83; albumen height, 0.77 and 0.91; yolk height, 0.78 and 0.77; incidence of blood and meat spots, 0.93 and 0.85. These results, although not consistent, present evidence for the genotype x period (or age of hen) interaction effects on egg quality traits.

Body Weight, Organ Weights, and Measurements: In the broiler industry, live weight is the most economically important trait, as the sale price of the birds is determined on this basis. Many hybrid chickens are available for sale to the commercial producer. Therefore, as with egg laying birds, random sampling tests of broiler chickens are in practice, so that the most profitable strain for a particular farm or location can be recommended. Thus, studies on interactions dealing with locations have received considerable emphasis. The age at which the live weights are measured, varies greatly among the reports. Therefore, an attempt will be made to mention the age at which live weight was taken, along with the corresponding reference, in the following list.

Following are the results of studies of interaction effects dealing with birds of different genetic background and various locations: significant for six-week weight in the ♂ ♂ but of low magnitude (2% of total variance), nonsignificant for the same trait in the ♀ ♀ and also unimportant for 10 weeks weight, breast angle, keel length, and shank length except for breast angle (which was significant in the ♀ ♀) but again only 2 percent of total variance, as reported by Merritt and Gowe (1956); indication of their presence on 10-week weight, observed by Weber and Le Roy (1956); a genetic bias of 0.03 for 32-week weight reported by Dickerson (1960); nonsignificant for weight at the end of a laying test and for adult weight, observed by Becker (1961) and Abplanalp and Marrou (1961), respectively; important for eight-week weight and no change in additive genetic variance with improved management level, as noted by Bowman and Powell (1962); significant interactions for two-, four-, six- and eight-week weights, observed by Cook *et al.* (1962); unimportant for 78 week weight, found by Abplanalp *et al.* (1962); 2.4 percent and 1.4 percent of total variance, respectively, for weights at eight and 32 weeks, estimated by Van Vleck *et al.* (1963); important for 18- and 58-week weights, found by Cook *et al.* (1963); significant for four- and six-week weights (reported as ration x location but ration and strain effects were confounded), observed by Aitken *et al.* (1964); no evidence for 10-week weight, found by Lewis and Blow (1965); important for weight at

160 days, noted by Nordskog (1966); significant for two-, four-, six-, and eight-wk. weights, investigated by Tindell *et al.* (1967a); important for eight-, 18- and 58-week weights, found by Tindell *et al.* (1967b); no evidence of stock x parent location interactions on 0-days, one-, five-, and eight-week weights in either sex except for one-week weight in ♀ ♀ and also no significant parent stock by growing location interactions at any of those ages except for one-week weight in both ♂ ♂ and ♀ ♀, reported by Tindell *et al.* (1968a); unimportant for two-, four-, six-, and eight-week weights, noted by Tindell *et al.* (1968b); important for eight- and fifty-eight-week weights, but not for 18-week weight, observed by Marks *et al.* (1969a); significant stock by parent stock location interactions for eight- and fifteen-week weights, but not for 58-week weights, and significant stock x growing location interactions for all eight-, 15- and 18-week weights in the study of Marks *et al.*, (1969c); and, finally, important interactions with parent stock locations for one-, five-, and eight-week weights in ♂ ♂ and for five- and eight-week but not one week weights in ♀ ♀; and interactions involving growing locations, significant for five- and eight-week but not for one week weights in ♂ ♂ and except at eight-week, not important for one- and five-week weights in ♀ ♀, reported by Marks *et al.* (1969b).

As expected, the results are not consistent. However, there is sufficient evidence for the important genotype x location interaction effects, so prior test performance is always necessary to recommend the best available stock for a growing location.

Studies of differential responses of stocks to year effects have revealed the following variable results: unimportant for adult weight (Abplanalp and Marrou, 1961); no evidence for 72 week weight (Abplanalp *et al.*, 1962); important for body weight gain to 280 days (Harms *et al.*, 1967); significant for eight-week but not for 18- or 58 week weight (Tindell *et al.*, 1967b); nonsignificant for 0-days and one-, five-, and eight-week weights (Tindell *et al.*, 1968a); important at two- and eight-week age in ♂ ♂ and at eight-week in ♀ ♀ but not at four- or six-week in ♂ ♂ or at two- or four- or six-week in ♀ ♀ (Tindell *et al.*, 1968b); and significant for eight-week but not for eighteen- or 58-week weight (Marks *et al.*, 1969a).

From these reports, one may expect the possibility of the occurrence of the differential responses of stocks with different genetic background x year effects. Thus, it is always advisable to recommend any stock of birds based on their performance for more than one year.

Okamoto *et al.* (1961) observed a significant genotype x season effect on the thyroid oxygen uptake but not on the thyroid weight in comparing White Leghorn and New Hampshire chickens and their reciprocal crosses. Varadarajulu (1966) reported a significant strain x season effect on body weight at four weeks of age. Further studies on interactions involving season of hatch effects, especial-

ly in countries where hatching is done for a long period of a year, would reveal interesting information.

Studies on interactions involving different levels of feeding have shown: significant effects on 147-day but not on 350-day weight (Hull and Gowe, 1962); significant influence, but of low magnitude on housing body weight (Gowe *et al.*, 1962); and no evidence of their presence in the body weights at 147 and 365 days of age (Hull *et al.*, 1963). Added to these findings, the components of variance of ♀ effects, the non-additive heredity and maternal effects were found by Mahmoud (1967) to be higher on the high plane than on the low plane. Besides, he observed that selection for eight-week body weight on a high plane of nutrition had no advantage over that on a low plane of nutrition but improvement of the genotypes for growth on a low plane did bring considerable improvement for growth on a high plane. The results of these studies indicate the importance of genotype x feeding level interaction on body weight in chickens.

Johnson and Abplanalp (1960), in their experiment on feeding two diets (crumbled and mash) to meat stocks, observed a significant stock x diet interaction effect on live weight at the end of their test in the pullets but not in the cockerels. A similar study by Merritt *et al.* (1960) dealing with mash *vs.* pellet feeding indicated the presence of a differential response of the strains to the diets for eight-, nine-, 10- and 11-week weights. However, Bray *et al.* (1962), in a study involving two rations, differing in their ingredients but similar in chemical composition, found no significant interactions for 62-day average weight, 62-day feed conversion, feed cost per pound at 62 days, estimated feed conversion to three pounds and estimated number of days to three pounds. These studies, dealing with differences in the consistency or the constituents of the rations, although they present variable results, do provide evidence for the presence of important interaction effects.

Experiments involving rations with different energy levels have revealed significant interaction effects on the growth rate to four-weeks of age in the study of Sibbald and Slinger (1963) but presented no evidence for these effects on eight-week body weight or body weight gain during the test period studied by Lillie *et al.* (1964) and Kondra and Sell (1966), respectively. In the former study, no strain x Ca level interactions were found. The reports are too few to draw any specific conclusions. Further investigations may reveal conclusively the importance of these interactions.

On comparisons of rations differing in combinations of high and low protein and energy levels, no strain x ration interactions were found by Kondra and Hodgson (1961) for six- or eight-week gains in weight, total feed efficiency, or protein and energy utilization. Complementary to these findings, no ration x strain interaction effects were observed by Kondra *et al.* (1962) for live weight at 8½ weeks of age or meat yield as percent of live weight or of dressed weight or of eviscerated weight. Studies involving rations varying only in their protein

levels have also been made. Results of study of interactions with these effects include: significant for average body weight (Deaton and Quisenberry, 1965); not important for live weight during the test period (Kondra and Sell, 1966); significant for weight gain in 280 days (Harms *et al.*, 1966; 1967); nonsignificant for eight-, 18- or 58- week weights (Marks *et al.*, 1969a) or at one-, five- or eight weeks of age (Marks *et al.*, 1969b). The results, again, are not consistent. However, the results of some of the studies indicate the importance of such differential responses.

Other studies dealing with different diets include: different levels of prota-mone, where a significant sire x treatment interaction on four-week weight was found by Kheireldin and Shaffner (1957); varying levels of vitamin B₆, resulting in the important interaction effects on four-week weights (Daghir and Balloun, 1963); graded amounts of thiamine, showing differential responses of sire-line and dam-line progeny for growth rate (Roberts, 1963); and finally, three levels of phosphorus and two breeds (commercial broilers and White Leghorns), where, significant interaction effects were observed by Gardiner (1969) for four-week weight, feed efficiency, percent bone ash, and plasma inorganic phosphorus. These reports, though few, do present evidence indicating the importance of the differential responses of genotypes to varying levels of the aforesaid essential nutrients.

Yao (1959), in an experiment dealing with slatted and litter floor housing, found no evidence for the presence of an interaction effect on mature body weight. Further, in a confinement *vs.* range comparison, Proudfoot and Gowe (1961) observed significant interaction effects for housing and 500-day body weights but not for March body weight in the year 1 and for none of the traits in year 2. The repeatability and genetic correlation estimates they reported were high for all the traits in both the years.

The results of experiments in determining the importance of interaction effects involving differences in floor space were: significant comb-type (single *vs.* heterozygous pea-combs) x brooder space interactions for body weight in one of the five experiments (Collins *et al.*, 1963); unimportant for two-, four-, six- or eight-week weights, except for four-week weight in ♂♂ (Tindell *et al.*, 1968b), and nonsignificant for adrenal weight, adrenal cholesterol, corticosterone or body weight at 57 days of age (Siegel and Siegel, 1969).

In cage *vs.* floor comparisons, an important interaction effect on March body weight was found by Gowe (1956), but it was not significant for adult body weight, as observed by Bailey *et al.* (1959).

Considering differences in cage density as the environmental factor, no significant differential responses for 142- and 427-day weights were found by Cook and Dembnicki (1966).

Comparisons of birds with different genetic background, housed separately or intermingled, showed no significant interactions for 160-day weight (Proud-

foot *et al.*, 1957); or for eight-, 32- or 55-week weights (King and Bray, 1959) or for eight- or nine-week weights (Hess *et al.*, 1960).

In general, the results do not indicate important interaction effects involving different systems of housing on body weight and related traits.

Among the studies dealing with different light regimes, significant differential responses of the stocks for 72-week weight but not for eight- or 20-week weights were observed by Siegel *et al.* (1963). Also, there interactions were found to be unimportant for three- or nine-week weights by Beane *et al.* (1965). From the results of these two reports, the interaction effects involving light regimes appear to be unimportant. However, further studies are suggested.

The operator, making different measurements has also been considered as one of the various environmental factors. As stated previously, the environmental factors could be as many as we can think of. Collins *et al.* (1964) observed significant operator x bird interactions for actual tibia circumference and shank length but not for breast angle. The results suggested repeated measurements for the first two traits but not for breast angle.

The problem of the differential responses to sex on the efficiency of selection is less acute in poultry than in the other farm animals because of the availability of large numbers of offspring of either sex. However, for the same reason, the intensity of selection is large with the former and, consequently, the presence of genotype x sex interactions, if any, will lead to extreme sexual dimorphism at a faster rate. Moreover, if there is any difference in the heritability estimates between the sexes, an advantage can be taken to further enhance the selection differential. No evidence of a source (stock) x sex interaction was noted by Hess *et al.* (1960) for eight- or nine-week weights. Kondra *et al.* (1962), in their study involving three broiler crosses, found no significant strain x sex interactions for live weight at 8½ wks of age or meat yield as a percent of live weight or of dressed weight or of eviscerated weight. Findings complementary to these were noted by Bray *et al.* (1962) for 62-day weight, 62-day feed conversion, feed cost per pound at 62 days, estimated feed conversion to 3 pounds and estimated number of days to 3 pounds in their fifth test. However, these interactions were found to be significant for 62-day weight, estimated feed conversion to 3 pounds and estimated number of days to 3 pounds but not for the other traits in their sixth test.

A critical study on sexual dimorphism in relation to genotype x sex interactions was made by Horton and McBride (1964). They reported important strain x sex as well as sire x sex interaction effects on four-week, eight-week, and gain from four- to eight week weights. The heritability estimates for the three traits in ♂♂ and ♀♀ were: 0.657, 0.249; 0.689, 0.506; and 0.656, 0.608, respectively. However, only those for four-week weight were significantly different in ♂♂ and ♀♀. Added to these figures, the genetic correlations reported by them were: 0.47, 0.49 and 0.49 respectively, for the three traits, considering the

strains as the genotypes; and with sires within strains as the genotypes, the corresponding figures were: 0.52, 0.48, and 0.47. In either case, each of the r_g values was reported to be significantly different from unity. Further, a significant interaction effect on eight-week weight was found by Lillie *et al.* (1964). But Siegel and Siegel (1969) observed varying results. Although none of the traits they studied were found to be influenced significantly in trial 1, they were important for body weight at 57 days of age, left adrenal weight (both adjusted and unadjusted for body wt.) and total adrenal weight (adjusted for body wt.) in trial 2.

Finally, the genetic correlation for 10-week body weight in White Leghorn birds was estimated to be 0.586 by Buvanendran (1969), indicating a genotype by sex interaction of important magnitude. The heritability estimates for the trait in ♂♂ and ♀♀ were 0.291 and 0.387, respectively, and 0.267 for sexual dimorphism (h^2_{M-F}). As stated by the author, the last estimate, though not significant, was of sufficient magnitude to make selection for sexual dimorphism effective.

From the review of these reports, the results are seen to be quite variable. However, there is enough evidence, especially in later years, to show the presence of interaction effects on sexual dimorphism.

Hematological Response: Washburn (1969) compared four stocks of chickens on two diets, a normal and another deficient in copper and iron and observed significant stock x diet and stock x age interactions on packed erythrocyte volume.

Resistance to Vitamin Deficiency: If certain strains resist vitamin deficiencies better than the others, differences in their responses would be observed in deficient diets but not in the normal diets and thus would indicate a genotype x diet interaction. Such differences in responses were observed by Lamoreux and Hutt (1948) in comparing resistant and nonresistant strains of White Leghorns for riboflavin deficiency and by Howes and Hutt (1952) for encephalomalacia caused by a vitamin E deficiency, the White Leghorns being more resistant than the Rhode Island Red and Barred Plymouth Rock chicks. Some of the other references dealing with varying levels of essential nutrients but not designed specifically to study the effects of deficiency have been quoted under the appropriate traits. For further details, see the papers by Hutt (1961a,b).

Avian Leucosis: Differential responses of three susceptible and three resistant groups of White Leghorns to three levels of exposure to lymphomatosis were observed by De Ome (1943). Similar observations were also reported by Hutt *et al.* (1945).

In a study of the influence of the location where selection for resistance to leucosis was practiced, King *et al.* (1952) exchanged two such populations located 900 miles apart. For results on mortality due to neoplasms, they concluded that resistance to leucosis in one locality would also prove useful in that respect in another locality; there was no evidence of genotype x location interactions. A

strain (resistant and susceptible) x age x severity of infection interaction on resistance to avian leucosis was observed by Hutt and Cole (1953). These evidences indicate the importance of the differential responses of strains to avian leucosis.

Other Diseases: Evidence for interactions between strains and body temperature for resistance to *Salmonella Pullorum* was noted by Scholes and Hutt (1942).

A differential response of non-interbreeding lines of *Hemophilus gallinarum* infection, using pause in egg production by laying hens as the criterion of measuring the susceptibility to the disease, was observed by Lerner *et al.* (1950).

Interactions involving lines of White Leghorn and *Eimeria tenella* infection for resistance to cecal coccidiosis, as measured by differences in mortality, was reported by Rosenberg *et al.* (1951). A similar report for the same disease was made by Edgar *et al.* (1951).

As an evidence for the presence of interaction effects on resistance to worm (*Ascaridia lineata* infestation, reference may be made to Ackert *et al.* (1935).

The importance of interaction effects has been generally indicated to be true for resistance to these diseases.

Heat Tolerance: Differential response to higher environmental temperatures, if it exists, would be of importance in the selection of strains or breeds for tropical regions. Such a differential response was noted by Hutt (1938) for resistance to heat in a comparison involving White Leghorn, Rhode Island Red, and Barred Plymouth Rock breeds as measured by differences in mortality. Further, an interesting observation of a breed x availability of drinking water interaction for heat tolerance was made by Fox (1951). In the absence of drinking water, the survival time was less for White Leghorn but when drinking water was provided, it was longer for the same breed, compared to Rhode Island Red and New Hampshire birds.

Behavioral Traits: The presence of interaction effects on the social behavior of birds, if it exists, would affect the efficiency of selection for the production traits. A significant strain x age at assembly interaction effect for social ranks was observed by Tindell and Craig (1959) in a comparison of six diverse strains of four breeds, housed separately or intermingled. Such a differential behavior was also hypothesized by Craig *et al.* (1965) from their experiment on selection for social dominance. Finally, differential escape responses of high- and low-weight lines of White Plymouth Rock chicks to a sudden loud noise, indicating the presence of line x method of rearing interactions were found by Phillips and Siegel (1966). These reports, though few, do indicate the importance of the interaction effects on the behavioral traits.

Turkeys: Body weight is the most important economic characteristic in the turkey business; sale price is solely determined on that basis. Asmundson and Lerner (1940) reared two strains of Bronze turkey ♂ ♂ and ♀ ♀ fed two ra-

tions differing in their protein levels and found no significant ration x strain or age x strain or sex x strain interactions for any of the following traits: body weights to 32 weeks of age, weight of pectoralis major, pectoralis minor, left gonad, bursa fabricii, length of keel, femur, tibiotarsus, and tarsometatarsus except one ration x strain effect for body weight, one age x strain for femur length and one sex x strain for bursa fabricii. However, the presence of a differential response of families to sex on 24-week body weight was noted by Shaklee *et al.* (1951). Further, Johnson and Asmundson (1957) observed significant sire family x hatch interactions on eight-week body weight, shank length, keel length, body depth, No. 1 breast width, and No. 2 breast width except for keel length in ♂♂ and No. 2 breast width in ♀♀. Becker (1963) found no significant hatch x line (Broad Breasted Bronzes) effects on eight-week body weight in ♂♂ or ♀♀ but he did find significant interaction for 24-week weight. They were important in ♀♀, however. No storage x line interactions were observed for either of the traits.

Friars and Singh (1967), in a study involving two small strains of turkeys, subjected eggs from different hatches to either refrigerated storage or refrigerated storage plus nitrogen gas in a closed environment. They observed significant strain x treatment ($P \leq .10$), strain x hatch ($P \leq .05$), and no strain x storage period interactions on hatchability of the eggs.

The reports on genetic x environmental interactions in turkeys are few and variable. Further studies in this species are needed to arrive at any broad conclusion.

Japanese Quail: Recently, research on quail has received some attention. Collins and Abplanalp (1968), in a comparison of the selected lines with reciprocal backcrosses to the control lines, observed a significant mating type x sex interaction on 8-week body weight but this was not true for carcass weight or liver weight. However there was no evidence of line x sex interaction for any of the traits. Another study was made by Kawahara (1968) on 31 sire families raised in three light regimes. He observed significant sire x light regime interactions on the age at sexual maturity and 12 to 16 week egg production but this was not true for the latter trait when adjusted for sexual maturity. It is desirable that more research be done on this subject with this species.

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