GENOTYPE BY ENVIRONMENT INTERACTIONS IN POULTRY

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SUMMARY

Genotype by Environment interactions (GxE) have been intensively investigated in poultry. Results indicate that greater GxE effects were associated with traits having lower heritabilities. It is possible that low heritability of a given trait results from an excess of non-heritable variance due to GxE rather then a lack of genetic variation. Data obtained from stock by location tests were not analyzed to the fullest extant because environmental specifications have not been measured and appropriate biometrical methods have not been used.

Commercial breeders have claimed to overcome GxE by having their customers adjust their husbandry to be optimal, rather then breeding specialized strains. However, the breeders' husbandry cannot always be applied, for reasons such as lack of resources, variation in market demands and poultry welfare regulation.

Definition of "environment" in regard to interaction with genotypes can be widen to include sexes and major genes. Interaction of sexes with genotypes has been found in meat-type chickens under extreme environmental conditions. In this case, sexes are regarded as "environments." Interaction of sexes with environments has been also reported. It appears that overall efficiency of broiler production can be improved by placing males in more optimal environments, and females in less optimal ones. Interaction of major genes for disease resistance with genotypes, i.e., "genetic background" was found to affect their level of expression. This type of interaction is essential to the utilization of gene transfer technology; an appropriate method for its analysis is described.

INTRODUCTION

The topic of Genotype by Environment interaction (GxE) and its application in practical breeding and production, has received a considerable attention since the early 50's. McBride (1958) related the initiation of this attention to Hammond's (1947) statement that "the character required is best selected for under environmental conditions which favor its fullest expression, and that once developed, it can also be used in other environments", and to Falconer's thesis that for this thesis to hold good, there should be no genotype-environment interaction. McBride classified GxE according to intra- and inter-population genotypes and micro- and macro-environmental factors and discussed their breeding implications in poultry. Dickerson (1960, 1962) also discussed the need and relevance of GxE studies, especially with poultry. Numerous reports on GxE studies in poultry have been published. Horst (1985) summarized 181 reports on GxE studies published between 1938 and 1981, and showed that the interactions were significant in about one-half of the cases.

A symposium entitled "Genotype x Environment Interactions in Poultry Production" was organized recently by P. Merat and the European "Breeding and Genetics" working group. Evidences for GxE were reviewed, new results were presented and their implications were discussed by prominent poultry geneticists. Therefore another review on GxE is not needed. Rather this paper will summarize briefly studies on GxE in poultry; point out generalized conclusions regarding GxE and related parameters; discuss the usefulness of biometrical methods to quantify GxE; extend the traditional definitions of "G" and "E", especially in view of the prospects of gene manipulation and transgenic animals.

DEFINITIONS OF ENVIRONMENTS AND GENOTYPES

McBride (1958) defined micro- and macro-environments. Micro-environments cannot be identified in most cases, since they result from the environmental fluctuations which occur, mostly by chance, within flocks. They are not initiated on purpose, but usually are unavoidable. The macro-environments are characterized mainly by being unique, e.g., geographic location, type of housing, climatic conditions, diet composition, etc. Macro-environments do not necessarily differ in their average effect on a given trait.

There are also two levels of genotype definition - within and between populations. The former relates to genetic variation within population, which is the basis for further selection, while the latter relates to genetic differences between established breeds or genetic stocks.

GxE with micro-environments is just a kind of "experimental error" in the breeding work (Horst, 1985). Hence breeders, as well as producers, try to reduce it through maximum uniformity of all management factors. Micro-environments will not be further discussed in this paper.

Macro-environments can interact with inter- as well as with intra-population genotypes. The former GxE means that a given established stock is more suitable than others to one environment but not to another one. The latter GxE indicates that breeding stock for use in a given environment should not be conducted in different environment. This is, of course, the opposite of Hammond's conclusion.

GxE IN POULTRY

1. Stock by Location interaction

Reports concerned with random sample tests of egg production stocks were summarized by, among others, Abplanalp and Menzi (1961), Horst (1985) and recently by Hartmann (1989a), who also summarized several broiler stock by location tests. Stock by Location interactions were found mainly for reproductive traits, and less so for production traits such as body and egg weight. In these studies, researchers addressed only the number of locations needed to reliably identify the stock with the best overall average. The breeding implications of the consistency of the interactions over years (Hull et al., 1963; Hartmann, 1989a) were neglected.

No use has been reported of the approach of characterizing each environment by the corresponding mean performance of all genotypes. This approach was suggested by Yates and Cochran (1938) and has been widely used in plants (see Becker and Leon, 1988, for review) and also in fish (Moav et al., 1976). By regressing the performance of each genotype at the various environments on the environments' means, the nature of GxE (linear, quadratic, etc.) and expected performance of a given genotype in an environment with a given average effect can be obtained (Wright, 1976). A better understanding and utilization of GxE can be achieved by multiple regression of genotypes' performances on physical and/or biological characteristics of each environment (Hardwick and Wood, 1972; Freeman, 1973; Westcott, 1986). In most random-sample tests, locations were characterized neither indirectly by average of performances, nor directly by environmental measurements, and consequently no useful conclusions have been made regarding the nature or prediction of GxE. While Merat (1989b) demonstrated that such predictions can be made, the needed detailed characteristics of environments in GxE studies are rarely available. Also comparisons between different GxE studies, or evaluation of presence or absence of GxE interaction, are not possible without exact characterization of the tested environments.

2. GxE with specified environments

More useful studies were conducted with genetically distinct egg-production stocks, or with a sample of sire families from a given stock, raised in environments differing by one of the followings: climatic conditions (Mukherjee et al., 1980); specifically controlled ambient temperatures (Bordas and Merat, 1984; Merat, 1989a); rearing systems (Patterson and Muir, 1984; Muir, 1985; Siegel et al., 1987); diets (Hull et al., 1963; Smith et al., 1989); age (Liljedahl, 1989); etc. Also in these studies, reproduction traits were found to be more affected by GxE than production traits. Some useful conclusions regarding adaptability of genotypes or breeding strategies for specific environments were made.

GxE studies with meat-type chickens were conducted mainly with inter-population genotypes raised in environments differing in diets (Marks and Britton, 1977; Sorenson, 1977; Cherry et al., 1978; Robbins, 1981; Laurin et al., 1985; Sorenson, 1985; Whitehead and Parks, 1988; Leenstra, 1989; Shalev and Borenstein, 1989). In several studies, environments differed in ambient temperatures (Cahaner and Leenstra, 1989), floor vs. cage rearing (Sorenson, 1989), induced stresses (Washburn et al., 1980; Dunnington et al., 1987), and lightening regimen (Cave et al., 1985).

GENERAL CONCLUSIONS FROM GxE STUDIES

1. Heritability and GxE

Greater GxE effects were associated with traits having lower heritabilities (Horst, 1985; Hartmann, 1989a). In layers - egg number, rate of lay, and mortality showed large GxE in all studies. Lower GxE effects, non-significant in some cases, were found for body weight and egg characteristics. Also in broilers, body weight was affected by GxE in some studies, but not in others. Abdominal fat percentage (of body weight), which are known to have very high heritability, has not been reported to be affected by GxE. While GxE affected body weights of lines selected divergently on abdominal fat percentage, no interaction was found for abdominal fat (Leclercq, 1983; Cahaner et al., 1985; Cahaner and Leenstra, 1989).

It has been often stated that traits with lower heritability are inclined to have large GxE (Horst, 1985). However, it seems that this statement should be read backwards - that traits which are inclined to high GxE have, consequently, low heritability. The evident negative association between high GxE and low heritability indicates that the latter results from an excess of non-heritable variation rather than a lack of heritable variation. Apparently traits such as egg production and mortality interact strongly with micro-environments within the populations and these influence the heritability estimates. This GxE is probably even greater in commercial breeding flocks than in experimental ones, and the variation due to GxE is added to the non-heritable variance and hence realized heritability is further reduced. It is possible, therefore, that the lower-than-predicted response to selection on traits with low heritability, compare to accurate prediction for traits with high heritability (Nordskog, 1977) can be attributed to large interactions between micro-environments and inter-population genotypes.

2. Optimal and sub-optimal environments

In those studies where one or several environments were more suitable ("optimal") for the chickens than others, GxE often resulted because genotypes which performed quite similarly in the optimal environments, responded differently to the sub-optimal ones (Merat, 1989a; Smith et al., 1989; Leenstra, 1989). The variation between genotypes under sub-optimal conditions, compared to their similarity under optimal ones, may be due to polymorphism in loci which affect adaptation to various stressors..This polymorphism prevails in modern stocks because it is not exposed during breeding programs. This situation is in agreement with the first half of Hammond's thesis: if optimal level of all environmental parameters is assured in practical production, then these conditions should also be kept in the population under selection. However, genotypes with lower performance in the optimal environment, are usually less affected by, or more able to compensate for sub-optimal environment or stress conditions (Cherry et al., 1978; Washburn et al., 1980; Cahaner and Leenstra, 1989). That is, of course, the opposite of what Hammond concluded.

Crosses should be excluded from the above generalization, because several studies have shown that crosses are less affected by sub-optimal conditions than "pure" lines, while pure lines perform similar to or better than the crosses in optimal environment (Hull et al., 1963; Barlow, 1981; Horst, 1985; Hartmann, 1989b; Orozco, 1989).

LIMITS TO MANIPULATION OF ENVIRONMENTS

Environments are usually regarded as alternative management systems, comprised of changeable components such as diet, rearing facilities, ambient temperatures, etc. Therefore, commercial breeders tended to follow Hammond's thesis. A commercial breeder may agree that GxE exist, but feel that he has overcome this problem by having his customers adjust their husbandry to a more optimal one - that used by the breeder. They could cite Abplanalp and Menzi, who wrote in 1961 that "perhaps more likely would be a systematic adaptation of management to the breeder's own strain". However, this Utopian approach does not hold in the following situations:

1. In many parts of the world, providing optimal environment means considerable capital investments: to control temperature and humidity, to ensure disease-free conditions, to supply balanced and highly concentrated diets, etc. It is not just a matter of training - the capital is not available. In some of the most heavily-populated parts of our world, sub-optimal environments for chicken production will prevail for years, necessitating specialized genotypes or crosses (Flock and Van Middelkoop, 1989; Horst and Mathur, 1989; Mathur and Horst, 1989; Van der Zijpp et al., 1989).

2. Market demands should also be considered as environments, and they require specialized genotypes (Flock and Van Middelkoop, 1989). White versus brown eggs are well known example for such a demand. More recently breeders face this problem with slaughter weight of broilers. The demand ranges from less than 1500g live weight in western Europe to about 3000g in Japan and markets were most broilers are deboned for further processing. Genotypes differing in their growth curve interact with these market-imposed environments, and specialized breeding is needed.

3. Welfare regulation regarding poultry management vary between countries. GxE has been found with floor vs. cage rearing of broilers (Sorenson, 1989), and with number of layers per cage (Muir and Patterson, 1984; Muir, 1985). Therefore, different regulated rearing systems may be expected to require different genotypes.

WIDER DEFINITIONS OF ENVIRONMENTS OR GENOTYPES

1. Interaction with sexes

Evidence has been reported for interaction of sex with genetic differences, or with environmental differences. The two possibilities are demonstrated in the following table, derived from Cahaner and Leenstra (1989). Final body weights are presented for males and females from a commercial broiler line and from a line selected for high abdominal fat. Chickens were kept either at a normal temperature (22°C) to 6 weeks or at a high temperature (32°C) to 8 weeks of age.

Genotype	Environment	Males	Females
Commercial broilers	Normal temp.	2260g	1875g
	High temp.	1510g	1767g
High Fat line	High temp.	1915g	1848g
	Normal temp.	2043g	1738g

When males and females of the same population rank differently in different environments, then sexes are the different genotypes. That is the case in the table above where broiler males were heavier than broiler females in normal temperature, and vise versa in the high temperature. Conversly High Fat males weighed more in normal temperature, while High Fat females weighed more in the high temperature. In both cases, although males and females were from the same population, their difference was not random and continuous as between intra-population genotypes. Rather it is a "fixed effect," such as between two distinct stocks, i.e., inter-population.

When males and females are ranked differently in two populations (for the same environment), the interaction is between inter-population genetic differences and sexes, where sexes can be regarded as two "environments". This is the case when comparing data collected in high temperature. Broiler females were heavier than broiler males, while High Fat males were heavier than High Fat females. The usual advantage of about 15% in body weight of males over females was reported to be reduced in sub-optimal environments such as cage rearing (Sorenson, 1989), low protein diet (Sorenson, 1977), and substitution of dietary carbohydrates with fat (Robbibs, 1981).

At present, producing chicks of one sex only is not possible. However, due to interactions between sexes and environments and/or stocks, and based on easy day-old sexing, it appears that overall efficiency of broiler production can be improved by placing males in more optimal environments, and females in less optimal ones.

2. Major genes and genetic background

For almost all economically important traits, inter-population and intra-population genotypes differ by a complex of many genes (polygenes). However, "major" (single) genes may also affect traits of interest. The genotypes of a major gene can interact with environments, as in the case of the dwarfing gene Dw and the Na gene for naked-neck (Bordas and Merat, 1984). However, they also can interact with polygenes which affect the same trait. These polygenes are not identifiable, are assumed to be scattered in the genome and are therefore referred also as "genetic background". One can see it as a matter of expression of continuous polygenic variation under different single gene genotypes, which can be regarded as different "fixed environments." On the other hand, it might be the case where single gene expression depends on the polygenes, i.e., on the "genetic background". This situation has been demonstrated by Martin et al. (1989) and Hartmann (1989b) regarding major genes affecting disease resistance in chickens. The benefit of the gene controlling resistance to leukosis varied greatly between different breeding populations. Similarly, Hartmann concluded that the feasibility of improving resistance to Marek's disease by making use of specific B locus alleles needs to be evaluated in crosses of particular breeding lines.

Although very important, Hartmann's conclusion that resistance to leukosis and Marek's disease is affected by major gene X polygenes interaction is not informative enough for breeders. First - the polygenic background is of a few distinct "pure" lines. They do not necessarily represent the polygenic variation within a heterogeneous population use for breeding. Second - the nature and magnitude of the interaction were not estimated. They are essential factors to be considered when major gene by genetic background interaction becomes an influential part of practical breeding program. Such an interaction is a very important aspect of transgenic animals, because the level of expression of foreign genes in the "host" depends on its interaction with the host's genome, i.e., the genetic background. A method was recently suggested (Elkind and Cahaner, 1986) to detect, characterize and quantify the interaction between major gene genotypes and polygenes. The experimental population is constructed by random matings of males and females heterozygotes for the major gene in question. The offspring population is comprised of families, each segregates to the three genotypes of the major gene. This two-way layout, in which the families are the random "genetic backgrounds", and they are orthogonal to the fixed genotypes of the major gene. Appropriate ANOVA facilitates the detection of interaction, as well as estimation of effects and components of variance. This method includes an interpretation of the interaction, which is based on the joint-regression approach suggest for GxE analysis by Yates and Cochran (1938). This method has already been utilized successfully in wheat (Beharav et al., 1988) and tomatoes (Elkind et al., 1990), and it can be applied easily to poultry.

CONCLUDING REMARKS

1. The performances of today's egg-production and meat-type stocks are approaching the biological limits of their main features - rate of lay and growth rate - when raised under optimal conditions. To achieve further improvement of the poultry industry world-wide, breeding programs have to look for genotypes who perform better in sub-optimal environments. Such programs have to rely on comprehensive GxE studies.

2. Methodology of GxE studies, especially where environments are locations, has to facilitate understanding of the biological nature of the interactions, and biometrical estimation of the effects of environmental factors on different genotypes.

3. The concept of GxE should be expanded to "major gene" by "genetic background" interactions. These interactions are essential to the utilization of gene transfer technology in poultry breeding.

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