GENOTYPE x ENVIRONMENT INTERACTIONS IN PIG BREEDING PROGRAMMES

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S T E L L I N G E N :

1) Genotype x milieu interacties tussen toets- en praktijkbedrijven worden veroorzaakt door grote verschillen in omstandigheden tussen praktijkbedrijven.

dit proefschrift

2) De effectiviteit van de Nederlandse fokprogramma's is aanmerkelijk te verbeteren door nauwkeurig en zuiver te corrigeren voor storende omgevingsinvloeden.

dit proefschrift

3) Levensgroei is een beter selectiekenmerk dan groei tijdens de mestperiode.

dit proefschrift

4) De selectie in varkensfokprogramma's dient te worden uitgevoerd onder omstandigheden die een goede afspiegeling vormen van de omstandigheden waarvoor het fokdoel geformuleerd is.

dit proefschrift

5) Het bestaan van genotype x bedrijf interacties betekent dat men zich in de varkensfokkerij niet moet beperken tot eigenprestatie-onderzoek.

dit proefschrift

6) De mogelijkheden voor toepassing van recurrent selectie in varkensfokprogramma's worden onderschat.

dit proefschrift

7) In de rundveefokkerij wordt bij de selectie op vleesproduktiegeschiktheid ten onrechte aangenomen dat genotype x bedrijf interacties afwezig zijn.

8) Het huidige systeem van richtprijzen voor biggen verhindert een alert reageren van vermeerderaars op veranderingen in vraag en aanbod van mestbiggen.

Merks, J.W.M. en Van Dijk, G., 1983.
Landbouwkundig Tijdschrift 95, nr. 3: 24-28.

9) De toepassing van elektronische levensnummers in de Nederlandse veehouderij maakt kwaliteitscontrole betrouwbaar en geloofwaardig.

10) Het drieluik van onderzoek, onderwijs en voorlichting in de landbouw wordt aangetast door de politiek van verzelfstandiging en privatisering.

11) Het is eerder de variatie dan het niveau van de vleeskwaliteit die van belang is voor de kwaliteitsbeleving door de consument.

12) Veehouders kunnen beter proberen het vertrouwen in het dierlijke produkt te versterken, dan te produceren tegen een nog geringere kostprijs.

13) Tegenstanders van genetische manipulatie onderschatten de kracht van moeder natuur.

Proefschrift van J.W.M. Merks
Genotype x environment interactions in pig breeding programmes.

Wageningen, 5 februari 1988.

J.W.M. Merks

Genotype x environment interactions in pig breeding programmes

Proefschrift
ter verkrijging van de graad van
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aan mijn ouders

aan Angela

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VOORWOORD

Dit proefschrift is voor een belangrijk deel tot stand gekomen door samenwerking tussen verschillende instellingen en bedrijven, in het bijzonder het Instituut voor Veeteeltkundig Onderzoek "Schoonoord" te Zeist en de Vakgroep Veefokkerij van de Landbouwuniversiteit te Wageningen. Het Produktschap voor Vee en Vlees te Rijswijk heeft een belangrijk deel van het onderzoek gefinancierd. Graag wil ik daarom een ieder bedanken die op enigerlei wijze heeft bijgedragen aan de totstandkoming van dit proefschrift. Enkelen wil ik hier met name noemen.

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CONTENTS

INTRODUCTION

A pig breeding programme generally consists of different levels in a pyramidal structure, indicated as nucleus, multiplication and commercial level. Selection takes place at all levels but improvements generated in the nucleus determine eventually the rate of annual genetic change. This genetic change is economically of importance at all levels but especially at the commercial level because of its relatively large number of animals. Therefore the breeding goal for selection on growth and carcass traits has to be defined at the level of commercial fattening.

Selection at nucleus level for growth and carcass traits is generally based upon performance testing, sometimes supplemented with sib information. These tests usually take place in central test stations under standardized environmental conditions to allow a fair comparison of the tested pigs. Aspects of standardized conditions are for example number of pigs per pen, feeding regime and medical care. However, these sophisticated conditions deviate from the conditions at the multiplication level and certainly also from the conditions at commercial fattening where the breeding goal is defined. As a consequence changes in rank order for genotypes between these environments may occur and lower the efficiency of pig breeding programmes. The same applies to breeding programmes with on-farm testing in the nucleus, because even on-farm tests are performed under special conditions, especially if they are combined with an auction of the tested animals.

Changes in rank order of genotypes between environments are indicated as genotype x environment interaction (G x E). Falconer (1952) proposed to measure changes in rank order between environments as the genetic correlation between the phenotypes for the same genotype in different environments. This concept is based on the assumption that the expression of identical traits may in fact not be controlled by the same sets of genes if G x E exists. If the occurrence of G x E is just a matter of scale, thus without affecting the ranking of breeding animals, the genetic correlation equals one. In that case G x E does not affect the efficiency of the breeding programme. However, at the end of the 1970's several non-unit estimates of genetic correlations between the different levels of pig breeding programmes were reported. Bampton et al. (1977), Standal (1977) and Schulte-Coerne and Simon (1978) reported poor genetic relationships between central and on-farm test results, while

Ketelaars (1979) reported poor genetic relationships between central test and commercial fattening results. These results were considered as serious indications for G x E in pig breeding programmes, although these comparisons concerned traits that are probably genetically not identical, e.g. daily gain on test and weight for age. In some studies even different sexes were present in the distinct environments. This G x E might also have serious drawbacks for Dutch pig breeding, e.g. for the Dutch herdbook breeding programme in which three levels may be distinguished; nucleus herds with testing at central stations, multiplication herds with on-farm testing and commercial herds with fattening pigs. In this study data of the Dutch herdbook breeding programme are used to gain more information on cause and effect of G x E.

The first main object of the project is the investigation of environmental effects in central test, on-farm test and commercial fattening results and the estimation of up-to-date genetic parameters for the traits measured at these levels of the breeding programme. The analyses of G x E may give biased results if the appropriate definitions of environmental effects and up-to-date genetic parameters are not used. Routinely collected central test and on-farm test data are used next to fattening data obtained from a progeny test of AI-boars started on commercial fattening herds. In chapter 2 the results of the research into environmental effects in central test data are presented and the genetic parameters for the traits measured at the test stations are reported. For on-farm test and commercial fattening data the environmental effects and genetic parameters are reported in chapter 3 and 5 respectively.

The second main object of the project is the analyses of G x E in the herdbook breeding programme. To investigate the problem of G x E in the herdbook breeding programme, the general description of G x E by Brascamp et al. (1985) is extended. The problem is analysed as the genetic correlations (r_G) between identical traits measured in the three levels and the genetic correlations (r_g) among identical traits measured in various environments within each of the three levels. A graphical presentation of the problem is given in chapter 1. As the traits used in the different levels of the breeding programme are not identical, the central test data are used to estimate genetic correlations between the various definitions of growth rate and carcass quality, all measured on the same animals (chapter 1). The genetic correlations within the nucleus, the multiplication and the commercial fattening level are reported in chapter 1, 4 and 5 respectively. The genetic correlations between these three

levels are reported in chapter 6. The data used are the same as the data used in the first part of the project.

Finally, in chapter 7 the estimated genetic correlations between and within the three levels are used to investigate the general consequences of G x E for the design and efficiency of pig breeding programmes.

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CHAPTER 1

GENOTYPE X ENVIRONMENT INTERACTIONS IN CENTRAL TEST AND CORRELATIONS BETWEEN SIMILAR TRAITS

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I. Central test.

GENOTYPE × ENVIRONMENT INTERACTIONS IN PIG BREEDING PROGRAMMES. I. CENTRAL TEST

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ABSTRACT

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In this first paper of a series, Dutch central test results are examined for genotype × environment interaction (G × E) and the data are further used to estimate genetic correlations between the various evaluations of growth and carcass quality, as used in the distinct environments of the breeding programme. G × E in pig breeding programmes is outlined as genotypes expressing different phenotypes in the distinct levels of the breeding programme or even in different environments within a level (e.g. herds).

In most studies on G × E, the expectation of genetic correlation between similar traits measured in different environments has been taken to be one. Estimated correlations between similar traits measured on central tested pigs in this study indicate however, that expectations should be smaller, especially for carcass characteristics. Genetic correlations of carcass backfat thickness (CB) with ultrasonic backfat thickness (UB), normally used in on-farm tests, were 0.61 and 0.57 for Dutch Landrace (NL) and Dutch Yorkshire (GY), respectively. Correlations of UB with backfat class, as used in commercial fattening, were 0.25 and 0.42. Genetic correlations of ham + loin % with type class were 0.60 and 0.94. In future analyses of G × E these differences in genetic background of the traits should be taken into account.

Genotype × batch and genotype × sex interactions were investigated for daily gain and feed conversion ratio. No significant interactions were found. However, for daily gain between arriving at the station and the end of the test, as well as for weight for age at the end of the test, genotype × batch interaction was significant ($P < 0.05$). The possible causes of these interactions are discussed. For slaughter characteristics genotype × month interactions were not of significance.

INTRODUCTION

A genotype × environment interaction (G × E) may be defined as a change in the relative performance of two or more genotypes measured in two or more environments. Interactions may therefore involve changes in rank order

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for genotypes between environments as well as changes in the absolute and relative magnitude of variance between environments. The interactions resulting from changes in variance between environments, pseudo-interactions (Dickerson, 1962), are of minor importance for the design of selection programmes. However, G × E that alters the phenotypic ranking of a series of genotypes between environments considerably hampers selection (Dickerson, 1962). In the literature this has resulted in a wide variety of estimates for genotype × environment interaction effects, reviewed by Pani and Lasley (1972) among others. In most studies genotypes are represented by breeds, groups of sires or sires. Environments are represented by environmental factors such as feeding regime or housing system, but also by sex or test environment.

Particularly in pig breeding, genotype × environment interaction may give problems. Breeding values for growth and carcass traits are generally estimated in specially designed test environments, as in central test and on-farm test environments. The aim of the breeding programme is, however, to improve the economically important traits of pigs fattened under commercial conditions. At the end of the 1970s Bampton et al. (1977), Standal (1977), Schulte-Coerne and Simon (1978) and Ketelaars (1979) reported poor genetic relationships between similar traits measured on sibs tested in different environments. Although these comparisons concerned traits that are probably not genetically identical (e.g. gain on test and weight for age), while sometimes different sexes were present in the various environments, these results were considered as serious indications of G × E in pig breeding programmes. This encouraged further research in the Dutch herdbook breeding programme on cause and effect of genotype × environment interaction.

In this first paper of a series, Dutch central test results are examined for G × E, since central testing is the main part of the breeding programme and the starting point of G × E studies. Further, the test data are used to estimate genetic correlations between the various evaluations of growth rate and carcass quality as used in the distinct environments of the breeding programme. As possible sources for G × E in centrally recorded fattening traits, genotype × batch and genotype × sex are investigated, while for slaughter characteristics genotype × month interactions are investigated. The paper begins with a general description of G × E to ensure a clear understanding of the stepwise approach in this study and to point out the gaps in the scientific study of the problem.

DESCRIPTION OF GENOTYPE × ENVIRONMENT INTERACTION IN PIG BREEDING PROGRAMMES

When describing the problem of genotype × environment interaction in pig breeding programmes, genotype is always represented by sires, but for the environment a distinction has to be made between three categories:

1. Specified factors such as feeding regime, housing system and sex.
2. Husbandry circumstances in general, e.g. herds or batches of tested pigs.
3. Levels of the breeding programme, particularly test versus commercial environments.

Any of these categories may be a factor in G × E. In this study sex is also considered as an environmental factor because it would be interesting to determine whether a genotype might lead to different phenotypic expressions in the different sexes. Interaction of genotype with a specific environmental factor may also be responsible for an interaction of genotype and herds if differences for this factor exist between herds. Interaction of genotype and herds may in turn, be responsible for interaction of genotype and level of the breeding programme, as the commercial environment includes different herds.

Research on interaction of genotype and specific environmental factors (e.g. King, 1963; Schnarr et al., 1982; Horn et al., 1984; Petersson, 1984) helps to decide whether it is necessary to match these factors in the central test with those under commercial conditions. But not all differences in environment between central test stations and commercial herds can be specified. It is even more difficult to specify differences in environment between commercial herds or between batches of pigs tested at a test station. Non-specific differences in husbandry may also give rise to G × E interaction, defined as genotype × herd or genotype × batch interaction.

In The Netherlands interaction of genotype × specific environmental factors has been investigated in the past for feeding level and sex (Minkema, 1970; Cöp et al., 1977; Minkema, 1982), but no serious indications were found for interactions. In this series, research on G × E is directed to the interaction of genotype × husbandry, and genotype × level of the breeding programme.

A short description of the G × E problem is given by Brascamp et al. (1985). On the basis of that general description, G × E can be described as in Fig. 1. The three blocks represent the three levels of the breeding programme; nucleus herds with testing at central stations, sow herds with on-farm testing and commercial herds with fattening pigs. The genotype × environment interaction between the different levels is represented by r_G, while r_g (analogous to the description of Brascamp et al., 1985) represents the genotype × environment interactions within a level of the breeding programme.

In the literature most estimates for genetic correlations between the genotypic value of a trait in different environments are, in terms of Fig. 1, estimates for r_{G_1}. This is the case for estimates by Bampton et al. (1977), Standal (1977), Schulte-Coerne and Simon (1978), Roberts and Curran (1981), Sönnichsen et al. (1984b), Groeneveld et al. (1984) and Ollivier et al. (1984). Estimates for r_{G_2} and r_{G_3} are scarce. Ketelaars (1979) estimated r_{G_2} for daily gain and backfat thickness, while Claus et al. (1984) estimated r_{G_2} and r_{G_3} for various traits. There are as yet no estimates for r_g, the genetic

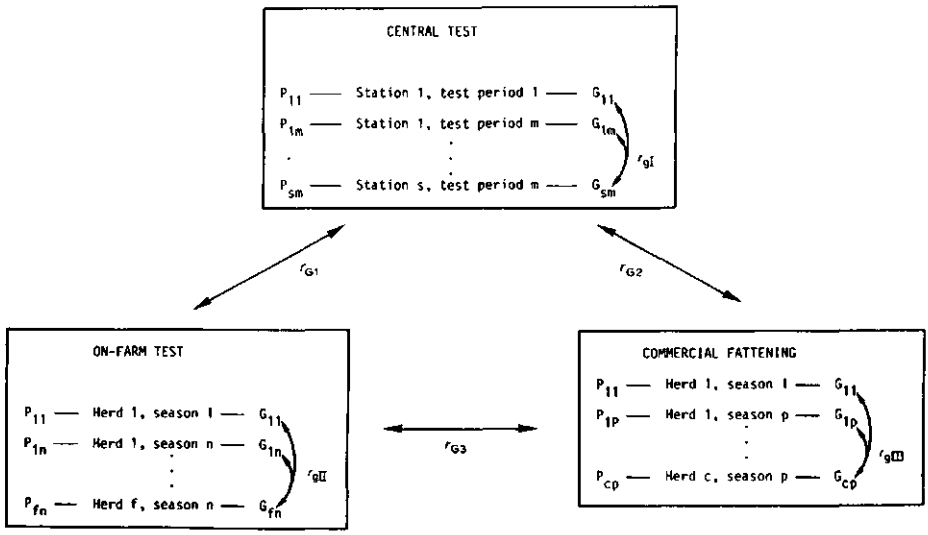

Fig. 1. Schematic description of the genotype X environment interaction problem in pig breeding programmes.

correlation between similar traits measured in various environments within a level of the breeding programme. As r_g gives a kind of upper limit for r_G (Brascamp et al., 1985), these estimates in particular would contribute to a better understanding of the G X E problem.

Good estimates for r_{G_1}, r_{G_2} and r_{G_3} as well as r_{gI}, r_{gII} and r_{gIII} are needed to study the impact of genotype X environment interaction in pig breeding programmes.

MATERIALS AND METHODS

Data were collected between April 1979 and August 1981 on two Dutch test stations in the herdbook breeding programme. Dutch Landrace (NL) and Dutch Yorkshire (GY) breeds were equally represented in both stations. The central test mainly concerned two boars and one gilt from each litter. Data collected were used for performance test as well as for progeny test. To conduct a reliable progeny test, 8—12 litters are tested per sire. In order to avoid very small sub-cells, only progeny of sires (all young A.I. boars) with three or more litters tested were used in the analyses, including about 90% of the tested animals. In Table I numbers of animals and sires are given for each breed/station combination.

Pigs were tested in batches. A batch consisted of a certain number of litters (15—30), entering the station within a short period and housed together in a particular unit of the station. No new pigs entered the unit until all the pigs in that unit finished testing. Animals arrived at the station at an average weight of 23 kg, were fed a mixture of standard composition

TABLE I

Numbers of Dutch Landrace (NL) and Dutch Yorkshire (GY) sires and progeny used in the analysis

	Station 1		Station 2	
	Sires	*Progeny*	*Sires*	*Progeny*
NL	141	2940	107	2512
GY	131	2564	102	3025

(9.4 KJ kg^{-1} net energy and 18% protein) according to weight and were housed individually. The test started at 25 kg. During the test both sexes were treated in the same way. Only gilts were slaughtered and dissected at the end of the test ($\geqslant$ 96 kg live weight).

To compare different evaluations of growth, daily gain on test was compared with daily gain as defined in the on-farm test and in commercial fattening. Daily gain on test (DGT) was calculated between 25 kg and live weight at the end of the test. In the on-farm test daily gain is measured on the basis of weight and age on the test day, so weight for age (W/A) was also calculated for the station-tested pigs at the end of the test. Daily gain in commercial fattening is calculated between arrival in the fattening pen and end of the fattening period. This definition was also used to calculate daily gain on station (DGS); daily gain between the moment of arriving at the station and the end of the test. Genetic correlations are estimated for these three traits measured on each of the tested pigs. Traits are corrected for environmental effects by including batch effects in the model (Merks, 1985).

Some other evaluations for growth rate are also of concern. In commercial fattening daily gain and feed conversion ratio are calculated on the basis of slaughter weight, estimated as 1.3 times carcass weight, instead of live weight at the end of the fattening period. To examine the effects of these differences in definition, daily gain on test and feed conversion ratio based on live weight were correlated with daily gain and feed conversion ratio based on calculated slaughter weight. The comparison was made for gilts, as only gilts were slaughtered.

Genetic variances and covariances for these different definitions of growth rate were estimated by "Henderson's method 3", as programmed by Harvey (1977), using Model 1. The analyses are carried out for each breed/station combination.

$$Y_{ijklm} = \mu + S_i + T_j + ST_{ij} + D_{k:ij} + R_l + e_{ijklm} \qquad \text{(Model 1)}$$

where

Y_{ijklm} = the record of the m-th progeny of the i-th sire and k-th dam with sex l, tested in batch j;

μ = population mean;
S_i = the (random) effect of the i-th sire;
T_j = the (fixed) effect of the j-th batch;
ST_{ij} = the (random) interaction effect of sire i and batch j;
$D_{k:ij}$ = the (random) effect of the k-th dam within the ij-th sire batch combination;
R_l = the (fixed) effect of sex l;
e_{ijklm} = random error.

Variance and covariance components for each breed were pooled over stations. Heritabilities (h^2), common environmental components (c^2) and genetic correlations between traits x and y ($r_{g_{xy}}$) were estimated as:

$$h^2 = \frac{4\sigma_S^2}{\sigma_S^2 + \sigma_D^2 + \sigma_{ST}^2 + \sigma_e^2} \quad (1)$$

$$c^2 = \frac{\sigma_D^2 - \sigma_S^2}{\sigma_S^2 + \sigma_D^2 + \sigma_{ST}^2 + \sigma_e^2} \quad (2)$$

$$r_{g_{xy}} = \frac{\sigma_{S_x S_y}}{\sqrt{\sigma_{S_x}^2 * \sigma_{S_y}^2}} \quad (3)$$

In the different levels of the breeding programme, different traits are used to evaluate carcass quality. On Dutch central test stations ultrasonic backfat thickness, carcass backfat thickness, ham + loin percentage and meat quality are used (Merks, 1985). In on-farm testing backfat thickness is measured ultrasonically, while in commercial fattening classification of carcasses according to EEC regulations is on the basis of backfat thickness and "type". With station test results it is possible to estimate the genetic correlations between these traits, all measured in the same environment. Ultrasonic backfat thickness is measured on boars, while carcass backfat thickness, ham + loin %, meat quality and classification are measured on gilts.

For the estimation of the correlation between these traits, carcass classification was decomposed into backfat thickness and a score for type. According to the classification for backfat thickness (De Boer, 1982, p.28), the class limits of 20, 25, 30 and 35 mm were used for the analyses. Nearly all the carcasses were within the weight range 70–80 kg. Type classes AA, A, B and C were transformed into 3, 2, 1 and 0, respectively. Ultrasonic backfat thickness was analysed as the average backfat thickness of the boar littermates. Variance and covariance components were estimated with Model 2 for each breed and pooled over stations. Genetic correlations are estimated according to (3):

$$Y_{ijm} = \mu + S_i + T_j + ST_{ij} + e_{ijm} \quad \text{(Model 2)}$$

Slaughter characteristics were corrected for environmental effects, including

in the model the effect of the time period (T_j) in which the pigs finished test. Time periods were defined according to the length of contemporary averages, considered to be best in correcting for environmental effects (Merks, 1985). As periods of 1 month were optimal for ultrasonic and carcass backfat thickness as well as for ham + loin %, month effects were also included in the model for the other slaughter characteristics.

The results of the analyses with Models 1 and 2 for the different traits were also used to study genotype × batch and genotype × month interactions. Genetic correlations between the genotypic value of traits measured in different batches or months were estimated. The subdivision in variance components given by Yamada (1962) for a random model (as a result of Yamada's description of the random model) was followed to estimate r_g:

$$r_g = \frac{\hat{\sigma}_S^2}{\hat{\sigma}_S^2 + \hat{\sigma}_{ST}^2 - \hat{\text{var}}\,(\hat{\sigma}_{S_j})} \qquad (4)$$

It was assumed that sire and error variances are equal in different environments ($\hat{\text{var}}\,(\hat{\sigma}_{S_j}) = 0$). This assumption had to be made, otherwise the method was not valid (Fernando et al., 1984).

The investigation of sire × sex interaction could not be done by including this interaction effect in Model 1. The small number of litters for each sire/batch combination would lead to confounding of effects. Therefore genetic correlations for daily gain and feed conversion ratio were estimated within litter between the average of the two boars and the gilt littermate. Variance and covariance components were estimated with Model 2 with the batch effect included.

As all variance and covariance components are estimated from indirect analysis (Harvey, 1977), negative variance components were set to zero before estimates of heritabilities, genetic and phenotypic correlations were made. Standard errors of these parameters were estimated according to formulae suggested by Tallis (1959) and Scheinberg (1966).

RESULTS

The comparison of different evaluations of traits starts with the comparison of different definitions for growth rate. Averages and standard deviations for these traits are given in Table II. In this table also phenotypic and genetic correlations between daily gain on test, daily gain on station and weight for age are given for each breed. Heritabilities and common environmental components are added. The genetic correlation between daily gain on test and daily gain on station does not differ from one. However, heritability (h^2) is higher and common environmental component (c^2) lower for daily gain on test. Genetic correlations for daily gain on test and daily gain on station with weight for age are somewhat smaller than one.

The results of the comparison of daily gain and feed conversion ratio based on measured live weight at end of test with the results based on calculated slaughter weight (1.3 times carcass weight) are given in Table III. The genetic correlations for Dutch Yorkshire indicate that fattening traits based on measured live weight are genetically the same traits as fattening traits based on weight calculated from carcass weight. The fact that genetic correlations of 0.89 and 0.86 are estimated from Dutch Landrace is mainly the result of lower genetic correlations (with large errors) at one station. At the other station genetic correlations for Dutch Landrace were comparable with correlations estimated in Dutch Yorkshire.

Phenotypic and genetic correlations between the different slaughter characteristics are given in Table IV. The ultrasonic backfat thickness measured on the boars correlates well with carcass backfat thickness (r_g = 0.60) and ham + loin % (r_g = −0.50) measured on the gilts. Correlations with the classified characteristics are weaker. However, high genetic correlations have been found between the carcass characteristics used for selection and the classified characteristics. For backfat thickness genetic correlations are around 0.80, for meat % (ham + loin % versus type) correlations range from 0.60 (NL) to 0.90 (GY).

TABLE II

Averages and standard deviations (S.D.) for different definitions of growth rate with phenotypic (above the diagonal) and genetic correlations (below the diagonal), heritabilities (at the diagonal) and common environmental components (c^2), measured on Dutch Landrace (NL) and Dutch Yorkshire (GY) pigs

		Average ± S.D.		DGT	DGS	W/A	c^2
		♂	♀				
DGT: daily gain on test (g)	NL	800 ± 50	753 ± 44	0.22 ± 0.05	0.68 ± 0.01	0.62 ± 0.01	0.13 ± 0.03
	GY	824 ± 52	786 ± 49	0.14 ± 0.05	0.69 ± 0.01	0.62 ± 0.01	0.11 ± 0.02
DGS: daily gain on station (g)	NL	685 ± 51	653 ± 45	0.98 ± 0.18	0.10 ± 0.05	0.82 ± 0.01	0.22 ± 0.03
	GY	707 ± 54	678 ± 49	0.99 ± 0.12	0.14 ± 0.06	0.81 ± 0.01	0.21 ± 0.03
W/A: weight for age (g day^{-1})	NL	556 ± 30	539 ± 26	1.00 ± 0.21	0.81 ± 0.17	0.09 ± 0.06	0.30 ± 0.03
	GY	569 ± 32	555 ± 29	0.84 ± 0.12	0.93 ± 0.09	0.20 ± 0.06	0.30 ± 0.03

TABLE III

Phenotypic and genetic correlations between fattening traits based on measured live weight and calculated live weight (1.3 times slaughter weight) at end of test

		Daily gain (g)	Feed conversion ratio (EW[a] per kg)
r_p	NL	0.87 ± 0.01	0.89 ± 0.01
	GY	0.88 ± 0.01	0.90 ± 0.01
r_g	NL	0.89 ± 0.06	0.86 ± 0.08
	GY	0.97 ± 0.03	0.97 ± 0.02

[a]EW = feed unit (FU) corresponding to about 8.8 kJ net energy.

TABLE IV

Phenotypic (above the diagonal) and genetic correlations (below the diagonal) between different slaughter characteristics for Dutch Landrace (NL) and Dutch Yorkshire (GY) pigs

		UB	CB	HL	MQ	T	BC
Ultrasonic backfat thickness (mm) (UB)	NL		0.18 ± 0.02	−0.13 ± 0.02	−0.03 ± 0.03	−0.09 ± 0.03	0.10 ± 0.03
	GY		0.17 ± 0.02	−0.15 ± 0.03	0.00 ± 0.02	−0.11 ± 0.02	0.11 ± 0.02
Carcass backfat thickness (mm) (CB)	NL	0.61 ± 0.13		−0.49 ± 0.02	−0.06 ± 0.03	−0.37 ± 0.02	0.39 ± 0.02
	GY	0.57 ± 0.10		−0.50 ± 0.02	−0.05 ± 0.03	−0.40 ± 0.02	0.41 ± 0.02
Ham + loin % (HL)	NL	−0.53 ± 0.17	−0.50 ± 0.13		−0.06 ± 0.03	0.42 ± 0.02	−0.37 ± 0.02
	GY	−0.44 ± 0.10	−0.60 ± 0.08		0.05 ± 0.02	0.48 ± 0.02	−0.42 ± 0.02
Meat quality (points) (MQ)	NL	−0.30 ± 0.20	−0.15 ± 0.18	0.10 ± 0.22		−0.05 ± 0.03	0.01 ± 0.03
	GY	0.43 ± 0.20	0.08 ± 0.20	−0.00 ± 0.18		0.02 ± 0.02	−0.02 ± 0.02
Type class (T)	NL	−0.04 ± 0.21	−0.62 ± 0.15	0.60 ± 0.16	−0.14 ± 0.23		−0.82 ± 0.01
	GY	−0.44 ± 0.17	−0.82 ± 0.13	0.94 ± 0.11	−0.30 ± 0.27		−0.86 ± 0.01
Backfat class (BC)	NL	0.25 ± 0.20	0.76 ± 0.13	−0.59 ± 0.16	0.17 ± 0.23	−0.91 ± 0.06	
	GY	0.42 ± 0.16	0.84 ± 0.14	−0.83 ± 0.10	0.11 ± 0.29	−1.00 ± 0.04	

TABLE V

Results of the analysis of sire × batch (S × T) or month interaction for each breed/station combination with significance level of the interaction effect and estimated genetic correlations

	Dutch Landrace				Dutch Yorkshire			
	Station 1		Station 2		Station 1		Station 2	
	sign	r_g[a]	sign	r_g[a]	sign	r_g[a]	sign	r_g[a]
Daily gain on test (g)	NS	0.84 ± 0.37	NS	1.00	NS	0.63 ± 0.39	**	0.35 ± 0.13
Daily gain on station (g)	***	0.06 ± 0.12	**	0.26 ± 0.14	*	0.18 ± 0.26	***	0.29 ± 0.11
Weight/age (g day^{-1})	***	0.16 ± 0.12	**	0.10 ± 0.14	**	0.20 ± 0.17	*	0.45 ± 0.16
Feed conversion ratio (EW per kg)	NS	0.62 ± 0.26	NS	1.00	NS	1.00	*	0.48 ± 0.18
Ultrasonic backfat (mm)	NS	0.60 ± 0.32	NS	1.00	NS	0.56 ± 0.26	NS	1.00
Carcass backfat (mm)	NS	0.63 ± 0.26	NS	1.00	NS	0.60 ± 0.25	NS	1.00
Ham + loin %	NS	1.00	NS	1.00	NS	0.98 ± 0.20	NS	1.00
Meat quality (points)	NS	1.00	NS	1.00	NS	0.31 ± 0.56	NS	1.00

[a]If $\sigma^2_{ST} \leqslant 0$, then r_g is set to 1.
NS, not significant; *P < 0.05; **P < 0.01; ***P < 0.001.

Genotype X batch interaction is investigated for feed conversion ratio and the different definitions for growth rate. For slaughter characteristics measured in Dutch test stations, genotype X month interaction is investigated. In Table V significance levels of the interaction effect tested against the dam effect, and estimated genetic correlations are given. There are clear indications for genotype X batch interactions only for daily gain on station and weight for age. For daily gain on test and feed conversion ratio, genotype X batch interaction is only of importance for Dutch Yorkshire pigs at Station 2. Genotype X month interactions are absent for carcass characteristics.

The genetic and phenotypic correlations for daily gain and feed conversion ratio, estimated within litter between the average of the two boars and the gilt littermate, are presented in Table VI. For Dutch Landrace the genetic correlations indicate the absence of genotype X sex interactions for daily gain as well as feed conversion ratio. The correlations for Dutch Yorkshire show a poor relation between male and female littermates. However, differences in genetic variance between boars and gilts are present for this breed.

TABLE VI

Phenotypic and genetic correlations between male and female with the genetic standard deviations for each sex/breed combination

		r_p	r_g	σ_s boars	σ_s gilts
Daily gain on test (g)	NL	0.21 ± 0.02	1.13 ± 0.22	7.6	9.5
	GY	0.17 ± 0.02	0.57 ± 0.18	8.5	12.0
Feed conversion ratio (EW per kg)	NL	0.20 ± 0.02	1.04 ± 0.23	0.03	0.03
	GY	0.18 ± 0.02	0.34 ± 0.18	0.03	0.05

DISCUSSION

The genetic correlation between daily gain on test and daily gain on station clearly indicates that those two traits are related to the same genotype. The rather low phenotypic correlation of 0.69 is probably due to the fact that daily gain on station is significantly affected by genotype X batch interaction (Table V), while this is not the case for daily gain on test. The only difference between these traits is the period between the arrival at the station and the start of the test, the adaptation period. Apparently this period is very important. For the data analysed, the adaptation period averaged 17 days, rather a long time to gain an average of 2 kg. The large change in environment, e.g. housing system, infection pressure and stall climate, to which the pigs have to adapt must be the reason for this. Although genetic correlations are almost equal to one, differences in genetic variance justify a rather long adaptation period such that carry-over effects of herds of origin are eliminated as much as possible.

If this adaptation period is the source of the genotype X batch interaction, genotype X batch or fattening period interactions may also be present in on-farm test results and commercial fattening data. A period similar to the pre-test period is included in those growth results. If station and on-farm tests are related without correction for this kind of genotype X environment interactions, they will probably give underestimated genetic correlations. Without correction for significant genotype X batch interactions, heritabilities and common environmental components for growth traits measured in central stations were overestimated (Merks, 1984). The question whether no correction of on-farm and commercial fattening results for genotype X batch or fattening period interaction is the reason for poor relationships between station and commercial results found in the literature, will be examined with Dutch herdbook data.

Genetic correlations for daily gain on test and daily gain on station with weight for age are lower than one. This means that daily gain measured in the central test and daily gain in the on-farm tests are genetically not exactly the same traits, as already anticipated by Standal (1977). This is mainly the result of the pre-test period, which is included in weight for age. Also Bampton et al. (1977) reported genetic correlations between weight for age in central testing and weight for age in on-farm testing that were higher than correlations between daily gain in central testing and weight for age in on-farm tests. Roberts and Curran (1981) however, could not confirm this.

It is not likely that these results are effected by genetic trend and the selection of A.I. boars. Correction for genetic trend is made by including batch effects in the model. The selection in the sires of the test litters is small, as only young boars were used to produce test litters. Based on the central test index, the selection intensities were 1.0 for NL and 0.68 for GY boars (Van Balkom, 1984). These selection intensities reduce the genetic variance by a very small percentage (Fimland, 1979), which has little or no effect on the correlations estimated.

Although genetic variation for killing out % exists (Minkema, 1970; Sönnichsen et al., 1984a) fattening traits based on live weight are, genetically speaking, no different from fattening traits based on carcass weight. Low genetic correlations between killing out % and daily gain or feed conversion ratio are the reason for this.

The genetic correlations in Table IV indicate that ultrasonic backfat (UB) measurements do not refer to the same set of genes as backfat measurements on the carcass (CB). Differences in measuring points, 5 cm beside the midline for UB and on the midline for CB, as well as differences in the technique, ultrasonic versus linear measurements, contribute to this. The estimated correlations are, however, of about the same magnitude as the correlations estimated by Sönnichsen et al. (1984b) between ultrasonic backfat thickness and carcass backfat thickness ($r_g = 0.88$) and between ultrasonic backfat thickness and weight of ham ($r_g = -0.62$). Each trait was measured on a group of station-tested pigs. For analysis of G X E in pig breeding program-

mes this means that the correlation of ultrasonic backfat thickness measured in on-farm tests with carcass backfat thickness measured in central tests, is not expected to be unity. An expectation of 0.6–0.8, according to the correlations in this paper, is more appropriate. So estimates of Standal (1977) (r_g = 0.65), Ollivier et al. (1984) (r_g = 0.63) and Sönnichsen et al. (1984b) (r_g = 0.69) between on-farm and central test results for backfat thickness should not be considered as indications of G × E. Groeneveld et al. (1984) however, estimated r_g = 0.20 between auction sales and central test results for backfat thickness.

The estimated genetic correlations between ultrasonic backfat thickness and ham + loin %, r_g = −0.50, are about the same size as the correlations between carcass backfat thickness and ham + loin %. Estimates of Bampton et al. (1977) (r_g = −0.41) and Roberts and Curran (1981) (r_g = −0.53) between ultrasonic backfat thickness in on-farm tests and lean % or weight of ham in central tests, are of the same size. However, Standal (1977) (r_g = −0.34) and Sönnichsen et al. (1984b) (r_g = −0.36) estimated lower correlations between these traits.

Genetic correlations between ultrasonic backfat thickness and classification results are rather weak. It is not surprising therefore that Claus et al. (1984) estimated a phenotypic correlation of −0.16 between ultrasonic backfat thickness of boars measured at auction sales and classification (% E + I) of progeny fattened in commercial herds. Correlations between carcass backfat and backfat class in Table IV are much higher. This is to be expected, as both are measured on the carcass. The genetic correlation of about 0.80 between carcass backfat thickness and backfat class is higher than Ketelaars (1979) estimated (r_g = 0.42) between carcass backfat thickness measured in central tests and backfat derived from classification results of pigs fattened in commercial herds. Also the correlation of 0.6—0.9 between ham + loin % and type class is somewhat higher than the correlation of r_g = 0.48 between similar traits derived from the results of Ketelaars (1979).

In most studies on G × E in pig breeding programmes the expectation of the genetic correlations between similar traits measured in different environments was one. However results in this study indicate that those expectations are too high. This is so particularly for carcass characteristics. Earlier Standal (1977) and Groeneveld et al. (1984) pointed to the different definitions for similar traits as an explanation for G × E. In future analyses of G × E more attention should be paid to comparing identical traits at the different levels of the breeding programme, or correction should be made for the differences in the genetic basis of the traits.

Genotype × batch interaction has already been discussed for daily gain on test and daily gain on station. For the estimation of these correlations it had to be assumed that sire and error variances were equal in the different environments, otherwise the estimates would have been biased (Fernando et al., 1984). However estimates of sire variance components for the growth traits showed large variation. Because of the small number of animals and

sires per batch, sire variance components were even often negative. So correlations in Table V should be considered only as an indication of the size of the genotype × batch or month interactions, not as genetic correlations between the genotypic values of the traits in different environments. Results on genotype × batch interactions for feed conversion ratio are comparable with daily gain on station. Slaughter traits are not affected by genotype × month interaction.

Results in the literature, of research on genotype × sex interaction, are rather different. In a station environment Smith and Ross (1965) reported sire × sex interactions for daily gain and backfat. Cook (1978) reported genetic correlations of about 0.8 between sexes for daily gain, feed conversion and fat depths. This included a possible interaction between sires and housing systems. Minkema (1970) derived a significant ($P < 0.05$) sire × sex interaction for ham % only ($r_g = 0.82$), while Minkema (1982) and Ollivier (1983) found no indications for genotype × sex interaction within a uniform environment for both sexes. Indications of genotype × sex interaction across environments (station—farm) are given by Roberts and Curran (1981) and Ollivier et al. (1984), who found higher genetic correlations for male–male comparisons than for male—female comparisons.

The results in Table VI show a good genetic resemblance for daily gain and food conversion ratio between male and female pigs of the Dutch Landrace breed. For Dutch Yorkshire pigs these genetic correlations indicate the existence of genotype × sex interaction. However, this interaction can probably be regarded as a pseudo-interaction according to Dickerson's terminology (1962). As shown in Table VI, differences in genetic variance were found between Dutch Yorkshire males and females. Differences in genetic variance between sexes for Dutch Landrace were much smaller. The absence of rank-order differences for breeding values could, however, not be proved because of the small number of pigs per sire/batch combination.

The preceding results indicate that genotype × environment interaction does not seem to be a major problem within central test environment. For daily gain on test sire × batch interaction is absent as long as an adaptation period is used. The indications found for sire × sex interactions within the Dutch Yorkshire breed for fattening traits should probably be regarded as pseudo-interactions.

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RESUME

Merks, J.W.M., 1986. Interactions génotype x environnement dans des programmes de sélection de porcs. *Livest. Prod. Sci.*, 14: 365—381 (en anglais).

Dans ce premier article, les résultats de testage obtenus aux Pays-Bas ont été examinés sous l'angle de l'intéraction génotype x environnement (G x E). Les résultats ont ensuite été utilisés pour estimer les corrélations génétiques entre les différentes estimations de la croissance et de la qualité de la carcasse qui sont utilisées dans les divers milieux de réalisation du programme de sélection. Dans ce programme, G x E apparaît dans les phénotypes différents qu'exprime un génotype aux divers niveaux du programme de sélection ou même lorsqu'à un niveau donné, il est placé dans des environnements différents (par exemple, les élevages).

Dans la plupart des études sur G x E, il était prévu qu'il y ait une corrélation génétique unique entre caractères similaires mesurés dans des milieux différents. Cependant, les corrélations entre caractères similaires estimées dans cette étude sur les porcs ayant subi le testage indiquent que les prévisions pourraient être plus faibles, en particulier pour les caractéristiques de carcasse. Les corrélations génétiques entre l'épaisseur de lard mesurée sur la carcasse (CB) et aux ultra sons (UB), utilisée normalement au cours du testage à la ferme, étaient de 0.61 et 0.57 respectivement pour les Landrace Néerlandais (NL) et Yorskshire Néerlandais (GY), tandis que les corrélations entre UB et la classe commerciale d'épaisseur de lard étaient de 0.25 et 0.42. Les corrélations génétiques entre le pourcentage de jambon + longe et la classe étaient de 0.60 et 0.94. Il faudrait tenir compte de ces différences d'ordre génétique pour ces caractères dans des analyses futures de G x E.

On a recherché les intéractions génotype x groupe et génotype x sexe pour la vitesse de croissance et l'indice de consommation. Aucune d'entre elles n'était significative. Cependant, l'intéraction génotype x groupe était significative ($P < 0.05$) pour la vitesse de croissance entre l'arrivée à la station et la fin du testage, ainsi que pour le poids ou l'âge à la fin du testage. Les causes possibles de ces intéractions sont discutées. Les intéractions génotype x mois pour les caractéristiques d'abattage étaient non significatives.

KURZFASSUNG

Merks, J.W.M., 1986. Genotyp- Umwelt-Interaktion in Schweinezuchtprogrammen. I. Stationstest. *Livest. Prod. Sci.*, 14: 365—381 (auf englisch).

In einer ersten Mitteilung wird an niederländischen Stationsdaten das Vorliegen von Genotyp x Umwelt Interaktionen (G x U) geprüft. Weiterhin werden genetische Korrelationen zwischen ähnlichen Merkmalen der Mastleistung und des Schlachtkörperqualität geschätzt, wobei die Mermale als in verschiedenen Umwelten erbrachte Leistungen aufgefasst werden. Dabei wird von einer G x U - Interaktion gesprochen, wenn bestimmte Genotypen verschiedene phänotypische Ausprägungen in unterschiedlichen Stufen eines Zuchtprogrammes oder in verschiedenen Umwelten (z.B. Betrieben) innerhalb einer Stufe aufweisen.

In einer Reihe von Untersuchungen über G x U - Interaktionen beträgt der Erwartungswert für die genetischen Beziehungen zwischen ähnlichen Merkmalen, die in unterschiedlichen Umwelten erhoben wurden, 1. Die eigenen Berechnungen ergaben deutlich geringere Korrelationen. Dies gilt insbesondere für Merkmale des Schlachtkörperqualität Die genetischen Beziehungen zwischen der Rückenspeckdicke am Schlachtkörper und der mit Hilfe von Ultraschall geschätzten Speckdicke (Merkmal aus Feldprüfung) betragen für die Landrasse bzw. für Yorkshire 0.61 bzw. 0.57, während die Korrelationen zwischen letzterem Merkmal und der in Klassen eingeteilten Rückenspeckdicke (Merkmal aus kommerzieller Mast) Werte zwischen 0.25 und 0.42 annehmen. Der genetische Zusammenhang von Schinkenlendeprozent mit der Typklasse schwankt zwischen 0.60 und 0.94. Somit sollte bei zukünftigen Analysen von G x U - Interaktionen dem unterschiedlichen genetischen "background" der Merkmale, Rechnung getragen werden.

Die Interaktionen Genotyp x Bucht und Genotyp x Geschlecht erwiesen sich für die Tageszunahmen (Prüfungsperiode) und die Futterverwertung als nicht signifikant. Lediglich für die tägliche Zunahme (bezogen auf die Ankunft in der Station bis Ende des Tests) und für die Lebenstagszunahme liess sich die Wechselwirkung Genotyp x Bucht mit einer Irrtumswahrscheinlichkeit von $P < 0.05$ absichern. Die möglichen Ursachen für diese Interaktionen werden diskutiert. Für Schlachtkörpermerkmale konnte keine signifkante Interaktion Genotyp x Monat nachgewiesen werden.

CHAPTER 2

ENVIRONMENTAL EFFECTS AND GENETIC PARAMETERS IN CENTRAL TEST

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GENOTYPE X ENVIRONMENT INTERACTIONS IN PIG BREEDING PROGRAMMES
II. Environmental effects and genetic parameters in central test.

Genotype × Environment Interactions in Pig Breeding Programmes. II. Environmental Effects and Genetic Parameters in Central Test

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ABSTRACT

Merks, J.W.M., 1987. Genotype × environment interactions in pig breeding programmes. II. Environmental effects and genetic parameters in central test. *Livest. Prod. Sci.*, 16: 215-228.

Environmental effects were investigated and genetic parameters estimated in central test results from Dutch Landrace and Dutch Yorkshire pigs, tested on two stations under a restricted feeding regime.

To investigate the environmental effects within test stations, different definitions of environmental effects were included separately in models for analysis of variance. Batch effects were significant ($P<0.001$) for daily gain and feed conversion ratio, and explained 7-12% of the variance. Backfat measurements and ham + loin percentage were significantly ($P<0.05$) influenced by month effects. Indications for an optimal environmental classification were shown only for daily gain and feed conversion ratio. For the carcass characteristics no balance could be found between chance and environmental fluctuations.

The estimated heritabilities for daily gain, feed conversion ratio and ultrasonic backfat thickness were 0.18, 0.21 and 0.28, respectively, if averaged over the two breeds, and were lower than those reported in the literature for pigs on restricted feeding. A different genetic structure (only A.I. data were used) and the chosen definition of environmental effects may have contributed to these differences. The differences between the two breeds in heritability, especially for ham + loin percentage ($h^2=0.34$ for Dutch Landrace and $h^2=0.75$ for Dutch Yorkshire), may be the result of the selection against halothane-positive animals in the first breed.

INTRODUCTION

Central tests were introduced to compare pigs across farms in a standardised environment using uniform feeding, housing and management. However, a complete standardisation of all environmental effects is impossible. Differ-

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ences in environment between stations are known (Flock, 1968; Pfleiderer, 1973; Andersen and Vestergaard, 1984), while the existence of seasonal effects on all traits recorded in central test is generally accepted; significant month or quarter effects were reported by Pfleiderer (1973), Lundeheim et al. (1980), Konrad (1981), Blum (1983) and Sönnichsen (1983). To correct test results for these environmental effects, contemporary averages are generally used (Lindhé et al., 1980). Little attention has been given to the application of the best linear unbiased prediction (BLUP) procedure for the evaluation of central test results, although Rönningen (1978), Kennedy (1982) and Bruns (1983) have initiated some discussion in this area.

In the Dutch herdbook breeding programme pigs are tested in batches (Merks and Minkema, 1983) within which the environmental variation should be small, as the pigs are housed together in a particular unit of the station and treated in the same way. Differences between succeeding batches might be small compared to differences between seasons. As the definition of environmental effects is of importance to obtain unbiased estimates of breeding values and genetic parameters (Van Vleck et al., 1961; Langholz, 1965b; Eikje, 1974), it also may affect the analysis of genotype (sires) by environment (test versus commercial) interaction. Therefore the purpose of this study was to investigate the environmental effects in central test results and to estimate suitable genetic parameters.

MATERIAL AND METHODS

The data used were those described by Merks (1986), i.e. data from two Dutch test stations in the herdbook breeding programme collected between April 1979 and August 1981. Dutch Landrace (NL) and Dutch Yorkshire (GY) breeds were equally represented in both stations. The traits measured at these stations and used in the selection index are described in Table I.

To investigate the environmental effects within test stations, batch, month and quarter effects have been included separately in models for analysis of variance, which were carried out with the LSML76 program of Harvey (1977). The average number of pigs, litters and sires for each of these classifications is given in Table II. The month and quarter effects were defined for each litter according to the month or quarter within year in which the first littermate finished the test. For carcass characteristics partition of the environmental effects according to the slaughter-day was also performed. Coefficients of determination for the environmental effects were calculated to show the reduction in sums of squares by the environmental classification used.

To determine the appropriate definition of environmental effects, the different classifications of the data were compared using the following criteria: (i) residual variance, (ii) genetic variance, (iii) heritability and (iv) the

TABLE I

Traits measured at Dutch central test stations

Name	Symbol	Calculation method
Daily gain on test (g day $^{-1}$) (boars and gilts)	DG	Average daily gain between 25 kg and end of test (96-105 kg)
Feed conversion ratio (EW kg $^{-1}$)[a] (boars and gilts)	FC	Feed conversion ratio between 25 kg and end of test
Ultrasonic backfat thickness (mm) (only boars)	UB	Average of 4 ultrasonic measurements 5 cm beside the central line of the back
Carcass backfat thickness (mm) (only gilts)	CB	Average of 4 linear measurements on each carcass half
Ham + loin percentage (%) (only gilts)	HL	Weight of ham and loin in both carcass halves as percentage of carcass weight
Meat quality (points) (only gilts)	MQ	Subjective score for meat quality based on colour and water holding capacity

[a]EW = 1 feed unit (FU) corresponding to about 1 kg feed.

average effective number of progeny per sire. The first three criteria were also used by Langholz (1965b) and Henningsson (1986) to find a balance between chance and environmental fluctuations by minimising the environmental variance and maximising the genetic variance, consequently maximising the heritability. The fourth criterion is appropriate in the context of genetic progress (PIDA, 1965; Dempfle, 1977) as the correlation between estimated and true breeding value of each sire depends, besides genetic and environmental variance, on the effective number of progeny.

TABLE II

Mean numbers of pigs, litters and sires within batches, months and quarters for each combination of breed and test station

	Station 1			Station 2		
	Batch	Month	Quarter	Batch	Month	Quarter
Dutch Landrace						
Pigs	37(19-72)[a]	113(70-189)	334(219-387)	21(5-37)	83(53-156)	269(234-335)
Litters	13(7-25)	38(35-57)	116(74-136)	7(2-13)	30(18-45)	94(79-117)
Sires	8(4-15)	15(10-22)	29(20-37)	5(2-9)	12(7-18)	22(16-28)
Dutch Yorkshire						
Pigs	52(12-61)	96(61-126)	292(264-326)	25(9-40)	100(53-152)	315(270-393)
Litters	11(5-22)	34(21-51)	102(92-117)	9(3-14)	34(21-51)	107(91-134)
Sires	7(2-13)	14(9-23)	25(23-30)	5(2-9)	10(7-14)	16(12-21)

[a]Minimum and maximum in parentheses.

For daily gain on test and feed conversion ratio the analyses were carried out within combinations of breed and station. Model 1, as indicated in the analyses by Merks (1986), was used and is provided below:

$$Y_{ijklm} = \mu + S_i + T_j + ST_{ij} + D_{k:ij} + R_l + e_{ijklm} \quad (1)$$

Where S, T, D and R represent the effects of sires, batches or time periods, dams and sexes respectively.

Data on ultrasonic backfat thickness were analysed using Model 1, excluding the sex effect. For carcass characteristics, Model 2 of Merks (1986) was used:

$$Y_{ijm} = \mu + S_i + T_j + e_{ijm} \quad (2)$$

The variation in weight at the end of the test was partly the result of genetic variation as pigs were weighed weekly; results were therefore not corrected for this small variation. For each breed, all results were pooled over stations as there was no heterogeneity between stations (Merks, 1984).

Coefficients of determination for environmental effects (abbreviated as $R^2(T)$) are calculated as follows (Searle, 1971):

$$R^2(T|\mu,S,R) = \frac{R(T|\mu,S,R)}{y'y - R(\mu)} \times 100 \quad (3)$$

Further, for each trait the results of the models with different classifications were used to estimate residual (σ_e^2) and sire variance (σ_S^2) components and to calculate the heritabilities. For the estimation of the heritabilities reference is made to Merks (1986). The average effective number of progeny per sire (n_e) is approximated by the number of σ_S^2 components in the model with the concerning classification.

An up-to-date set of genetic parameters were estimated using the classification found to be most appropriate. The variance and covariance component estimates for each breed were pooled over stations to estimate heritabilities, common environmental components and genetic-, phenotypic- and common environmental correlations. The common environmental correlation represents the environmental causes of similarity between full sibs x and y and is estimated according to:

$$r_{c_{xy}} = \frac{\sigma_{D_{xy}} - \sigma_{S_{xy}}}{\sqrt{(\sigma^2_{D_x} - \sigma^2_{S_x})(\sigma^2_{D_y} - \sigma^2_{S_y})}} \quad (4)$$

As all variance and covariance components were obtained by indirect analysis (Harvey, 1977), negative variance components were set to zero before heritabilities and correlations were computed. Standard errors of the parameters were estimated as was done in the earlier analyses (Merks, 1986).

TABLE III

For each breed/station combination the means and standard deviations for the traits measured at Dutch central test stations (April 1979-August 1981)

	Dutch Landrace				Dutch Yorkshire			
	Station 1		Station 2		Station 1		Station 2	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Boars								
DG (g day $^{-1}$)	796	46	805	46	813	50	835	49
FC (EW kg $^{-1}$)	2.74	0.19	2.59	0.16	2.67	0.10	2.46	0.15
UB (mm)	12.4	1.5	11.5	1.1	11.4	1.3	10.9	1.0
Gilts								
DG (g day^{-1})	751	43	756	45	778	46	792	48
FC (EW kg^{-1})	2.92	0.21	2.81	0.18	2.81	0.18	2.62	0.17
CB (mm)	23.7	2.7	22.7	2.5	22.5	2.4	22.3	2.5
HL (%)	46.7	1.3	46.8	1.3	47.0	1.3	47.1	1.3
MQ (points)	7.0	0.8	7.1	0.6	7.6	0.5	7.6	0.5

RESULTS

Table III gives averages and standard deviations for the traits measured. The differences between boars and gilts were as expected and significant ($P<0.001$) for DG and FC in all analyses. The Dutch Yorkshire was clearly superior to Dutch Landrace for all fattening and slaughter traits.

Batch, month and quarter effects were significant ($P<0.001$) for DG, FC and UB; however, the results in Table IV show that batch effects explained the largest part of the variance for each of these traits. Sire variance components are of the same magnitude for the batch as for the month classification. With a further enlargening of the classes, the sire variances increased rapidly, but little or no correction was made for the environmental effects. Error variances are not tabulated as they were independent of the chosen environmental classification. Dams were always nested within the sire by environment interaction and therefore the dam variance components included the effects not explained by the chosen classification.

Some of the results of the analyses on carcass characteristics are shown in Table V. With increasing size of the environmental classes the effective number of progeny per sire were respectively 5.25, 5.78, 6.53, 6.93 and 7.40 for Dutch Landrace and 5.79, 6.35, 7.18, 7.57 and 8.13 for Dutch Yorkshire. For all carcass characteristics the largest reduction in variance was obtained with the smallest environmental unit, the slaughter-day, but this classification resulted in low effective numbers. Without correction for environmental effects, the highest heritabilities and effective numbers were obtained, but the largest residual variances occurred.

TABLE IV

Results of the analyses with different environmental classifications for daily gain, feed conversion ratio and ultrasonic backfat thickness (for each breed pooled over stations)

	Dutch Landrace					Dutch Yorkshire				
	$R^2(T)$	σ^2_S	σ^2_D	h^2	n_e	$R^2(T)$	σ^2_S	σ^2_D	h^2	n_e
Daily gain (DG)										
Batch	11.3	88	295	0.22	17.5	12.0	61	256	0.14	18.7
Month	4.6	82	425	0.20	20.3	8.5	59	463	0.12	21.8
Quarter	1.4	122	500	0.26	21.5	1.6	164	538	0.31	23.2
No correction	-	317	535	0.61	21.9	-	458	591	0.76	24.8
Feed conversion ratio (FC)										
Batch	7.4	0.0015	0.0052	0.23	17.5	8.5	0.0010	0.0038	0.19	18.7
Month	2.9	0.0015	0.0055	0.21	20.3	3.8	0.0011	0.0048	0.19	21.8
Quarter	1.3	0.0015	0.0062	0.21	21.5	1.7	0.0018	0.0055	0.29	23.2
No correction	-	0.0056	0.0070	0.69	22.9	-	0.0066	0.0062	0.89	24.8
US backfat thickness (UB)										
Batch	8.7	0.066	0.499	0.18	12.1	9.7	0.085	0.244	0.31	12.6
Month	6.4	0.096	0.481	0.26	14.1	3.8	0.082	0.261	0.29	14.8
Quarter	1.4	0.135	0.541	0.34	14.9	1.3	0.122	0.281	0.41	15.7
No correction	-	0.334	0.560	0.75	15.8	-	0.231	0.294	0.71	16.8

T: NS, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

For the classification found to be most appropriate, genetic parameters were estimated. The heritability estimates in Table VI for DG, FC and MQ were obtained with the batch effect in the model, while for UB, CB and HL the month effect was included. The estimated genetic and phenotypic correlations are given in Tables VII and VIII for boars and gilts respectively. For boars the batch effect was included in Model 1, for gilts the month effect in Model 2. The estimated common environmental correlations for the traits measured on the boar littermates are given in Table IX.

DISCUSSION

Environmental effects and their appropriate classification

The results in Table IV clearly reveal batches as environmental units for DG and FC, although Langholz (1965a), Lundeheim et al. (1980), Konrad (1981), Blum (1983) and Sönnichsen (1983) reported significant month effects for these traits. This batch effect is probably caused by the same treatment of all pigs within a batch for feeding, climate regulation and management. In test systems without a batchwise approach, seasonal effects may be more pronounced but their contribution to the variation will be smaller than the contribution of batch effects.

TABLE V

Results of the analyses with different environmental classifications for carcass backfat thickness, ham + loin percentage and meat quality (for each breed pooled over stations)

	Dutch Landrace					Dutch Yorkshire				
	$R^2(T)$	Sign. T	σ_S^2	σ_r^2	h^2	$R^2(T)$	Sign. T	σ_S^2	σ_r^2	h^2
Carcass backfat (CB)										
Slaughter-day	11.8	NS	0.77	5.51	0.49	12.9	NS	0.84	4.84	0.59
Batch	10.5	NS	0.75	5.47	0.48	11.2	NS	0.79	4.88	0.55
Month	3.6	*	0.79	5.54	0.50	8.0	*	0.84	5.03	0.57
Quarter	1.7	***	0.70	5.54	0.45	2.9	*	0.79	5.06	0.54
No correction	-	-	1.10	5.62	0.65	-	-	0.84	5.08	0.57
Ham + loin % (HL)										
Slaughter-day	13.7	*	0.10	1.39	0.27	10.9	NS	0.35	1.24	0.88
Batch	10.7	NS	0.12	1.46	0.31	10.4	*	0.26	1.21	0.70
Month	5.5	***	0.13	1.41	0.34	3.1	*	0.29	1.24	0.75
Quarter	3.4	***	0.16	1.42	0.40	1.3	*	0.30	1.25	0.77
No correction	-	-	0.20	1.46	0.48	-	-	0.37	1.26	0.91
Meat quality (MQ)										
Slaughter-day	10.8	NS	0.020	0.50	0.15	13.2	NS	0.001	0.24	0.02
Batch	9.5	NS	0.034	0.46	0.28	11.0	NS	0.013	0.24	0.20
Month	3.9	NS	0.032	0.46	0.26	3.3	NS	0.012	0.24	0.19
Quarter	2.1	***	0.039	0.46	0.32	0.9	NS	0.011	0.25	0.17
No correction	-	-	0.043	0.46	0.34	-	-	0.015	0.25	0.23

Sign. T: NS, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

The batch effect also explained the largest part of variance for UB. However, the differences between batch and month classification are small for the sire and dam variance components. Least squares means for months (Fig. 1) indi-

TABLE VI

Estimated heritabilities (h^2) and common environmental components (c^2) with their standard errors for Dutch Landrace and Dutch Yorkshire pigs

	Dutch Landrace		Dutch Yorkshire	
	h^2	c^2	h^2	c^2
DG	0.22 ± 0.05	0.13 ± 0.03	0.14 ± 0.04	0.11 ± 0.03
FC	0.23 ± 0.05	0.14 ± 0.03	0.19 ± 0.05	0.13 ± 0.03
UB	0.26 ± 0.07	0.26 ± 0.03	0.29 ± 0.07	0.14 ± 0.03
CB	0.50 ± 0.09		0.57 ± 0.09	
HL	0.34 ± 0.08		0.75 ± 0.10	
MQ	0.28 ± 0.08		0.20 ± 0.07	

TABLE VII

Estimated phenotypic (above the diagonal) and genetic (below the diagonal) correlations with their standard errors for traits measured on boars

	DG	FC	UB
DG	Dutch Landrace	−0.88 ± 0.01	0.04 ± 0.02
	Dutch Yorkshire	−0.85 ± 0.01	0.14 ± 0.02
FC	−1.07 ± 0.04		0.02 ± 0.02
	−1.02 ± 0.08		−0.01 ± 0.02
UB	−0.07 ± 0.19	0.16 ± 0.19	
	−0.31 ± 0.30	0.23 ± 0.22	

cate that the environmental effects on UB consist partly of season effects. Significant month effects for UB in central test results are also reported by Sönnichsen (1983).

TABLE VIII

Estimated phenotypic (above the diagonal) and genetic (below the diagonal) correlations with their standard errors for traits measured on gilts

	DG	FC	CB	HL	MQ
DG	D. Landrace	−0.89 ± 0.01	−0.12 ± 0.02	0.16 ± 0.02	0.03 ± 0.03
	D. Yorkshire	−0.86 ± 0.01	−0.04 ± 0.02	0.06 ± 0.03	0.05 ± 0.02
FC	−0.94 ± 0.08		0.20 ± 0.02	−0.24 ± 0.02	−0.04 ± 0.02
	−1.04 ± 0.02		0.14 ± 0.02	−0.17 ± 0.03	−0.07 ± 0.02
CB	−0.04 ± 0.19	0.16 ± 0.18		−0.49 ± 0.02	−0.06 ± 0.03
	−0.41 ± 0.14	0.37 ± 0.12		−0.50 ± 0.02	−0.05 ± 0.02
HL	0.08 ± 0.22	−0.09 ± 0.21	−0.50 ± 0.13		−0.06 ± 0.03
	0.17 ± 0.13	−0.25 ± 0.12	−0.60 ± 0.08		0.05 ± 0.02
MQ	0.09 ± 0.23	−0.08 ± 0.22	−0.15 ± 0.18	0.10 ± 0.22	
	0.42 ± 0.20	−0.48 ± 0.18	0.08 ± 0.20	−0.01 ± 0.18	

TABLE IX

Estimated common environmental correlations (r_c) with their standard errors for traits measured on at least two littermates

	Dutch Landrace	Dutch Yorkshire
DG-FC	−0.78 ± 0.04	−0.78 ± 0.03
DG-UB	0.11 ± 0.09	0.38 ± 0.10
FC-UB	−0.06 ± 0.10	−0.36 ± 0.12

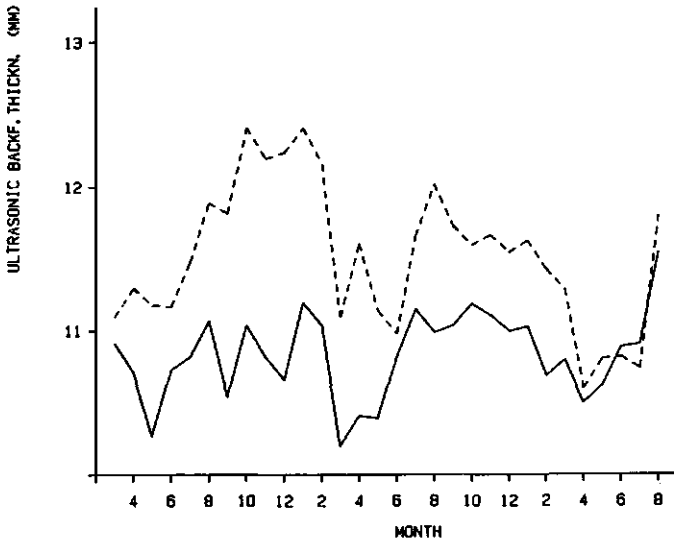

Fig. 1. Least squares month means for UB, estimated on Station 2 for Dutch Yorkshire (—) and Dutch Landrace (- - -).

For CB and HL only month and quarter effects were significant, which is in agreement with the results of Langholz (1965a), Flock (1968), Pfleiderer (1973), Lundeheim et al. (1980), Konrad (1981), Blum (1983) and Sönnichsen (1983). The coefficients of determination for month effects have the same magnitude as those reported in the literature.

For MQ the differences in results between batches, months and quarters were small, especially for the variance components. The classification according to slaughter-days resulted in small σ_S^2 and a low n_e, although the coefficients of determination have the same size as those reported by Pfleiderer (1973), Lundström et al. (1979) and Bergmann and von Lengerken (1982) for the effects of slaughter-day on meat colour. No obvious conclusions can be derived for the environmental effects on MQ; however, the results in the literature (e.g. Bergmann and von Lengerken, 1983) refer to slaughter-day effects.

The environmental effects on DG and FC coincided mainly with the batch effects. For carcass characteristics seasonal fluctations may be more important. For each of the traits analysed, the enlargening of the environment classes went together with an increase in sire variances, n_e and residual variances, while $R^2(T)$ decreased. Without correction for environmental effects the values for h^2 were the highest; these high heritabilities may be caused by confounding of season and sire effects as the progeny of a sire was tested within a period of 3–6 months. For carcass characteristics the numbers of animals tested is probably too small to obtain classes large enough to be genetically representative and at the same time representative for seasonal effects. The lack of

homogeneity of the variances, especially for the slaughter-day and batch classification, may also have contributed to the discordant results. To deal with this Ollivier et al. (1980) standardised the variance within batches, but this may change the genetic variance if the data of different batches are combined. It might be that there is no best classification, or that the best classification may differ with time.

Apart from the choice of an appropriate definition of environmental effects the procedure used to correct for the environmental effects is important. If contemporary averages are used, biased estimates for the environmental effects are obtained. Another method is exponentially smoothed moving averages, where the contemporaries are weighed according to the time interval between the proband and the contemporaries (Cook, 1977). This has the advantage that the size of environmental classes is dependent on the throughput of animals. This procedure is of special interest if the size of the classes is not very critical. However, unbiased correction for environmental effects is only possible if environmental and genetic effects are included simultaneously in the estimation procedure. For the estimation of genetic parameters the superiority of REML (Thompson, 1982) is well known. Unfortunately, REML computer programmes are not yet available for the analysis of large data sets with two random effects and a hierarchical family structure, although Meyer (1986) recently presented an algorithm for this kind of analysis.

Genetic parameters

The genetic parameters estimated may be influenced by the choices of the environmental effects included in the analyses, but such an effect is of minor importance, as was the case for the effect of environmental classification on genetic variance (Tables IV and V). The estimated heritabilities for DG, FC and UB were rather low in comparison with estimates in literature for pigs on restricted feeding (e.g. Pedersen, 1977; Ollivier et al., 1980; Kintaba et al., 1981): part of the differences in heritabilities may be the result of the genetic structure of the data. Most heritabilities for traits measured at central test stations were estimated in a model with sires nested within herds (tested pigs were sired by a natural service boar). With such a data structure, it is very difficult to separate genetic and environmental (herd) effects as shown by Vangen (1984). In the Dutch herdbook breeding programme, only progeny of A.I. boars were allowed to be centrally tested, making herd of origin effects negligible and genetic variances unbiased. Paradoxically, the selection among A.I. boars may have contributed to the reduced heritabilities, but as selection intensities for individual index traits were low (Van Balkom, 1984), a reduction of $< 10\%$ is to be expected.

Heritability estimates for CB and HL are in agreement with the results in the literature (e.g. Bampton et al., 1977; Pedersen, 1977; Kintaba et al., 1981)

for pigs on a restricted diet. However, the differences in heritability between the two breeds are large: the estimates for Dutch Landrace were lower than those derived from test results of this breed between the years 1966 and 1970 (Merks and Minkema, 1983), which were 0.56 and 0.58 for CB and HL respectively. These differences are probably the result of selection for halothane-negative animals in this breed, which started when about 22% of the animals were halothane-positive. In 1981 about 10% were positive (Knap and De Gier, 1984). However, the decrease in heritability was larger, especially for HL, than that predicted by Brascamp et al. (1980). On the other hand, the decrease in heritability for meat quality was less than expected, although the decrease in phenotypic variance (45%) was in correspondence with these model calculations.

The estimated correlations for DG and FC are in agreement with correlations reported in the literature for traits measured in pigs on restricted feeding (e.g. Hanset and Van Snick, 1973; Pedersen, 1977; Merks and Minkema, 1983). The correlations between the different slaughter characteristics are also within the range of results in literature, as discussed earlier (Merks, 1986) while the estimated common environmental correlations resemble the results of Sönnichsen (1983).

Differences in correlations between the two breeds were small and not significant. According to Brascamp et al. (1980), selection against halothane-positive animals would affect only the correlations between CB and HL and between MQ and HL, both becoming more negative. Only the genetic correlation between CB and HL has become more negative ($r_g = -0.50$ *vs.* -0.35 on the basis of the earlier mentioned results), while the correlation between HL and MQ has become positive ($r_g = +0.10$ *vs.* -0.25). These differences are not significant.

The changes in the parameters estimated, compared with earlier estimates, and the differences in parameters between breeds, stress the importance of regular estimation of genetic parameters. Up-to-date parameters are not only of the highest importance in obtaining continuous maximum genetic progress, but also for a more correct evaluation of genotype × environment interaction across levels of the breeding programme.

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RESUME

Merks, J.W.M., 1987. Interactions génotype × environnement dans les programmes de sélection porcine. II. Effets de l'environnement et paramètres génétiques dans le contrôle en stations. *Livest. Prod. Sci.*, 16: 215-228 (en anglais).

On a recherché les effets de l'environnement et estimé les paramètres génétiques dans les résultats du contrôle en station de deux races, Landrace néerlandais et Yorkshire néerlandais. Les porcs, alimentés de façon rationnée, étaient testés dans deux stations.

Différentes définitions des effets de l'environnement ont été inclues séparément dans des modèles d'analyse de la variance, de façon à rechercher ces effets intra-station. L'effet bande était significatif ($P < 0.001$) pour la vitesse de croissance et l'indice de consommation, et expliquait 7-12% de la variance. Les mesures d'épaisseur de lard et le pourcentage de jambon + longe étaient significativement influencés ($P < 0.05$) par l'effet du mois. Des indices pour une classification optimale des facteurs du milieu n'ont été obtenus que pour la vitesse de croissance et l'efficacité alimentaire. En ce qui concerne les caractéristiques de carcasse, aucun équilibre ne pouvait être établi entre les variations dues au hasard et celles liées à l'environnement.

Les estimations de l'heritabilité de la vitesse de croissance, de l'indice de consommation et de l'épaisseur de lard aux ultra-sons étaient respectivement de 0.18, 0.21 et 0.28 en moyenne pour les deux races, et inférieures aux valeurs rapportées dans la bibliographie pour des porcs alimentés de façon rationnée. Une structure génétique différente (seules des données d'insémination artificielle ont été utilisées) et la définition choisie pour les effets de l'environnement peuvent contribuer à ces différences. Les écarts d'héritabilité entre les deux races, en particulier celle du pourcentage de jambon + longe, 0.34 pour les Landrace néerlandais et 0.75 pour les Yorkshire néerlandais, peuvent résulter de la sélection contre les animaux positifs à l'halothane qui est pratiquée dans la première de ces races.

KURZFASSUNG

Merks, J.W.M., 1987. Genotyp×Umwelt-Interaktion in Schweinezuchtprogrammen. II. Umwelteffekte und genetische Parameter in der Stationsprüfung. *Livest. Prod. Sci.*, 16: 215-228 (auf englisch).

An Stationsprüfungen von zwei Rassen, der niederländischen Landrasse und dem niederländischen Yorkshire, wurden Umwelteffekte analysiert und genetische Parameter geschätzt. Die Schweine wurden auf zwei Stationen unter einem rationierten Fütterungsregime geprüft.

Um die Umwelteffekte innerhalb der Prüfungsstationen zu untersuchen, wurden verschieden definierte Umwelteffekte getrennt in die Modelle der Varianzanalyse aufgenommen. Durchgangseffekte waren für tägliche Zunahme und Futterverwertung signifikant ($P<0.001$) und erklärten 7-12% der Varianz. Rückenspeckdicke und % Schinken und Kotelett waren signifikant ($P<0.05$) durch Monatseffekte beeinflusst. Anzeichen für eine optimale Umweltklassifikation wurden lediglich für tägliche Zunahme und Futterverwertung gefunden. Für Schlachtkörpermerkmale konnte kein Ausgleich zwischen zufälligen und umweltbedingten Fluktuationen gefunden werden.

Die geschätzten Heritabilitäten für tägliche Zunahme, Futterverwertung, und Echolotspeckdicke betrugen 0.18, 0.21 und 0.28 als Mittel über beide Rassen und lagen niedriger als bisher in der Literatur für rationiert gefütterte Schweine ausgewiesen. Die unterschiedliche genetische Struktur (nur Besamungsdaten wurden einbezogen) und die gewählte Definition von Umwelteffekten mögen diese Unterschiede verursacht haben. Die Unterschiede der Heritabilitäten zwischen den beiden Rassen, besonders für Schinken und Kotelett-%, mit 0.34 für Landrasse und 0.75 für Yorkshire, könnten das Resultat der Selektion gegen halothanpositive Tiere in der Landrasse sein.

CHAPTER 3

ENVIRONMENTAL EFFECTS AND GENETIC PARAMETERS IN ON-FARM TEST

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III. Environmental effects and genetic parameters in on-farm test.

ABSTRACT

On-farm test records from 31268 Dutch Landrace (NL) gilts and 27997 Dutch Yorkshire (GY) gilts and boars were analysed to investigate environmental effects and to estimate genetic parameters. In addition to weight (WEIGHT) and backfat thickness (UB), weight for age (W/A), a score for weight corrected for age (SC W), a score for backfat thickness corrected for weight (SC UB) and the index (INDEX) were analysed. The analyses were performed within breed-sex combinations.

Seasonal effects, analysed by month x year classes, were significant ($P < 0.001$) but negligible for their contribution to the variance (for INDEX < 0.6 %). Herd effects were significant ($P < 0.001$) and explained 9 to 20 % of the variance within herdbook region, depending on the characteristic. A part of these herd effects was due to differences in sire selection. Within herdbook regions these differences were small owing to intensive use of AI. However, across regions indications were found for moderate genetic herd differences. Inspector effects also contributed to the variation; about 20 - 30 % of the herd differences for INDEX were attributable to inspectors.

The heritabilities for W/A, UB, SC W, SC UB and INDEX were 0.12, 0.28, 0.13, 0.39, 0.26 for NL and 0.18, 0.23, 0.19, 0.27, 0.22 for GY. The genetic correlations between W/A and UB were 0.25 for NL and 0.48 for GY and between SC W and SC UB respectively 0.02 and 0.24.

INTRODUCTION

On-farm testing of young breeding gilts and boars is a common practice in many breeding programmes (e.g. Hamelin et al., 1976; ; Standal, 1977; Scholling et al., 1981; Hudson and Kennedy, 1985). In The Netherlands on-farm testing started at the end of 1968. To rank the tested animals, a performance index was constructed (Minkema, 1973). A serious drawback of on-farm testing is its low accuracy (Hofstra and Minkema, 1973). In particular herd effects may bias the genetic evaluation of the tested animals. An appropriate correction of the test results for herd effects may increase the accuracy and decrease the bias. Scholling et al. (1981) compared different methods to correct for herd effects, but the results did not show an improvement in accuracy. Hudson and Kennedy (1985) introduced a linear model for evaluation of on-farm

test results that provided best linear unbiased predictions of breeding values. These breeding values are suitable for selection across herds, especially in case of intensive use of AI, and inclusion of records from relatives will increase accuracy considerably.

The purpose of this paper was to investigate the environmental effects in on-farm test results and to estimate genetic parameters. Only with these results it is possible to analyse genotype (sires) by environment (central test versus on-farm test) interaction properly. This will be done in a future paper of this series.

MATERIAL AND METHODS

Data of Dutch Landrace (NL) and Dutch Yorkshire (GY) gilts and boars tested in the herdbook field testing programme were used. The gilts were tested between May 1980 and December 1983, whereas the boars were tested between May 1982 and December 1983. On-farm testing is used frequently in the Dutch herdbook breeding programme. Herds with pure breeding have to use the on-farm test to obtain registered breeding stock. Because of the intensive use of AI, the test is performed mainly with gilts. Only young boars destined for natural service are tested on-farm, potential AI-boars are sent into the central test (Merks, 1986).

In the on-farm test pigs are weighed and their backfat thickness is measured ultrasonically at an age of about 190 days. On basis of age, weight and backfat thickness a performance index is calculated. This index is a linear combination of two scores; a score for weight corrected for age, and a score for backfat thickness corrected for weight (Minkema, 1973). The corrections are performed with the average within animal regression of weight on age and of backfat thickness on weight.

For this study the measurements of weight (WEIGHT) and backfat thickness (UB), weight for age (W/A), the two scores (SC W, SC UB) and the index (INDEX) were analysed. Because the index was constructed for each of the four combinations of breed and sex, the data were split up in the four sets. The number of data for each breed-sex combination are given in Table I. The total number as well as the number of records per herd for Dutch Landrace boars was too low to offer substantial information. The records of NL-boars were therefore not used in this study. Of the other breed-sex combinations a selected set of data was

used. Programme limitations restricted the number of classes of fixed effects. For each breed-sex combination only data of herds with at least a 100 animals tested were used. Owing to this the average number of pigs per herd increased considerably, which enabled a more sensitive analysis of environmental effects within and between herds. The numbers of records used are tabulated in Table I. About 99 % of the sires represented in the selected data were AI-boars.

Table I. Initial and used numbers of records, sires, litters and herds for each breed-sex combination (NL = Dutch Landrace, GY = Dutch Yorkshire).

	Initial data sets				Data sets used		
	NL ♂	NL ♀	GY ♀	GY ♂	NL ♀	GY ♀	GY ♂
records	3068	54905	23146	27876	31268	11169	16828
sires	191	643	496	346	279	218	215
litters	1635	21754	10293	9061	12586	4708	5374
herds	244	610	492	396	76	69	78
pigs/litter	1.88	2.52	2.25	3.08	2.48	2.37	3.13
pigs/herd	13	90	47	70	411	162	216

Analyses were performed within each breed-sex combination with the LSML76 programme (Harvey, 1977). Season effects were investigated with model 1. Month and year in which the test was performed were included as seasonal effects. For the seasonal effects coefficients of determination ($R^2(M,Y,MY|\mu,S,H)$) are calculated according to (1). The notation of Searle (1971) was followed for the reduction in sums in squares.

$$\underline{y}_{ijklm} = \mu + S \times H_i + M_j + Y_k + M \times Y_{jk} + \underline{D}_{l:ijk} + \underline{e}_{ijklm} \qquad \text{(model 1)}$$

Where,

y_{ijklm} = the record of the m-th animal
$S \times H_i$ = the (fixed) effect of sire x herd class i
M_j = the (fixed) effect of month j
Y_k = the (fixed) effect of year k
$M \times Y_{jk}$ = the (fixed) interaction effect of month j and year k
$D_{l:ijk}$ = the (random) effect of the l-th litter within the i-th sire x herd class and within jk-th month x year class
e_{ijklm} = random error

$$R^2(M,Y,MY|\mu,SH) = \frac{R(M,Y,MY|\mu,SH)}{y'y - R(\mu)} \times 100 \qquad (1)$$

The herd effects were investigated with model 2. Seasonal effects could not be included in the model because of programme limitations. The data were pre-corrected with the least squares means from model 1 and the degrees of freedom were adapted to this precorrection.

$$y_{hijkl} = \mu + YB_h + S_{i:h} + H_j + S \times H_{ij:h} + D_{k:hij} + e_{hijkl} \qquad \text{(model 2)}$$

In addition to model 1,

YB_h = the (fixed) effect of the year of birth h
$S_{i:h}$ = the (random) effect of sire i
H_j = the (random) effect of herd j
$S \times H_{ij:h}$ = the (random) interaction effect of sire i and herd j

The intra-herd correlations (t) were estimated according to:

$$t = \frac{\sigma_H^2}{\sigma_S^2 + \sigma_H^2 + \sigma_{SH}^2 + \sigma_D^2 + \sigma_e^2} \qquad (2)$$

The genetic part of the differences between herds was also evaluated. Sires were assumed to be used randomly across herds and the covariance between genetic and environmental herd-level was assumed to be absent. In the analyses with model 3 environmental (HE) and genetic (HG) differences between herds are included in σ_{H*}^2. The genetic herd differences include differences due to sire (HS) as well as to dam (HD) selection.

$$\underline{y}_{ij} = \mu + \underline{H}^*_i + \underline{e}_{ij} \qquad \text{(model 3)}$$

$$\sigma^2_{H^*} = \sigma^2_{HS} + \sigma^2_{HD} + \sigma^2_{HE} = \sigma^2_{HG} + \sigma^2_{HE} \qquad (3)$$

If variance components for the herd effects are obtained from direct analysis with model 2, environmental differences and differences due to dam selection are included (4). So $\sigma^2_{HS} = \sigma^2_{H^*} - \sigma^2_{H}$ is an indication for genetic herd differences due to sire selection. To facilitate interpretation, σ^2_{HS} is compared to the overall herd differences according to (5).

$$\sigma^2_{H} = \sigma^2_{HD} + \sigma^2_{HE} \qquad (4)$$

$$h^2_{HS} = \frac{\sigma^2_{H^*} - \sigma^2_{H}}{\sigma^2_{H^*}} = \frac{\sigma^2_{HS}}{\sigma^2_{HG} + \sigma^2_{HE}} \qquad (5)$$

Because the responsibility of the herdbook breeding programme is spread over four regional herdbooks, also analyses were performed with herd effects nested within their region. The results of the extended models 2 and 3 were used to calculate t and h^2_{HS} after correcting for regional differences.

The effects of inspectors who weighed the animals and measured the backfat thickness were investigated also. Generally, each inspector supervised a group of herds, and only in exceptional cases did another inspector visit the herd. Therefore, the test results gathered by the inspector who generally visited the herd were analysed with model 2, in which herds were nested within inspector effects. Coefficients of determination for inspector ($R^2_{(I/H)}$) effects were calculated according (6).

$$R^2_{(I/H)} = \frac{R(I|\mu,S,H)}{y'y - R(\mu)} \times 100 \qquad (6)$$

Genetic parameters were estimated for each breed-sex combination for all characteristics, except for WEIGHT because its meaning for selection is negligible. Variances and covariances were estimated by "Henderson's method 3", using model 2. Sires were nested within their year of birth to remove bias due to genetic trend. For these analyses the data, precorrected for seasonal effects, were used. Standard errors of the different parameters were estimated as in earlier analyses (Merks, 1986).

RESULTS

For each breed-sex combination the averages and overall standard deviations are listed in Table II. At the same test age (191 days), Dutch Yorkshire gilts (GY♀) were heavier and had thinner backfat than Dutch Landrace gilts (NL♀). At the same test age, boars were heavier than gilts, each having similar backfat thickness. Because of the different score and index coefficients used to calculate the results, the differences in scores and index are not clearly related to differences in weight and backfat thickness.

Table II. Averages ($\bar{x}$) and overall standard deviations (S.D.) for each breed-sex combination.

		NL ♀		GY ♀		GY ♂	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
Age at test (days);	AGE	191.6	14.5	191.5	15.1	190.7	12.7
Weight at test (kg);	WEIGHT	100.6	11.1	104.6	11.9	115.2	13.0
Backfat thickness (mm);	UB	13.1	2.3	12.0	2.1	12.0	2.1
Weight/age (g/day);	W/A	526	55	547	60	605	66
Score for weight;	SC W	0.992	1.076	1.177	0.904	1.336	1.018
Score for backfat;	SC UB	-0.939	0.892	-0.642	0.814	-0.846	0.752
Index (points);	INDEX	13.45	2.31	13.24	1.82	14.36	2.14

The analyses of seasonal variation with model 1 showed significant ($P < 0.001$) month x year interactions for each trait in the three data sets, except in GY ♀ for SC W ($P > 0.05$). Coefficients of determination for the seasonal effects, including month, year and month x year effects ranged between 0.4 % for SC W and 1.2 % for WEIGHT. For INDEX, seasonal variation explained 0.6 % of the variance.

Herd effects are an important source of variation ($P < 0.001$) for on-farm test results. Table III shows that 10 to 26% of the variance across regions in scores and index originated from herd differences. The inclusion of region effects in the analyses diminished the size of the herd effects only to a small extent. However, genetic differences between herds (h^2_{HS}) due to sire selection

were large if region effects were not included in the model, but within a region differences due to sire selection were moderate or small.

Table III. Intra-herd correlations (t) and proportion of herd differences due to sire selection (h^2_{HS} ± standard error) estimated across or within herdbook regions.

	Across regions		Within regions	
	t	h^2_{HS}	t	h^2_{HS}
NL ♀				
WEIGHT	0.17	0.08 ± 0.20	0.15	-0.06 ± 0.24
UB	0.16	0.25 ± 0.17	0.12	0.06 ± 0.23
W/A	0.22	0.31 ± 0.16	0.16	0.20 ± 0.19
SC W	0.23	0.31 ± 0.16	0.17	0.21 ± 0.19
SC UB	0.12	0.18 ± 0.18	0.09	0.05 ± 0.23
INDEX	0.10	0.18 ± 0.18	0.09	0.18 ± 0.20
GY ♀				
WEIGHT	0.13	0.07 ± 0.23	0.13	0.07 ± 0.24
UB	0.14	0.21 ± 0.20	0.10	-0.04 ± 0.26
W/A	0.20	0.23 ± 0.19	0.16	0.01 ± 0.25
SC W	0.21	0.24 ± 0.19	0.16	0.01 ± 0.25
SC UB	0.14	0.24 ± 0.19	0.11	-0.02 ± 0.26
INDEX	0.11	0.18 ± 0.21	0.11	0.14 ± 0.22
GY ♂				
WEIGHT	0.19	0.10 ± 0.21	0.19	0.08 ± 0.22
UB	0.22	0.32 ± 0.16	0.17	0.06 ± 0.23
W/A	0.22	0.11 ± 0.20	0.19	-0.06 ± 0.25
SC W	0.24	0.17 ± 0.20	0.19	-0.09 ± 0.26
SC UB	0.26	0.38 ± 0.14	0.20	0.08 ± 0.22
INDEX	0.19	0.08 ± 0.22	0.19	0.05 ± 0.23

Inspector effects were investigated in a selected data set (about 70 % of the records) with one inspector for each herd. WEIGHT and UB were especially influenced by inspector effects. For scores and INDEX the inspector effects R^2 (I/H) explained 1-5 % of the total variance. The inspector effects were not

significant if tested against the herd effects, except for SC UB in GY ♀ and GY ♂. Correction for inspector and herd effects, with herd effects nested in the inspector effects, reduced error variances similar to that obtained with correction for only herd effects. For INDEX, about 20-30 % of the differences between herds originated from inspector differences. For UB and SC UB this proportion was higher in GY than in NL.

Genetic and phenotypic parameters were estimated for each breed-sex combination from the results of model 2. Sire x herd interaction was significant ($P < 0.001$) for each characteristic if tested against the litter effect. The variance and covariance components for GY♀ and GY♂ were pooled because their estimates were similar. The heritabilities in Table IV were low for W/A and SC W but moderate to high for the other characteristics. The heritability for SC UB was significantly higher for NL than for GY, the opposite applied to SC W. The heritabilities for the index were similar for NL and GY. There are some differences between the two breeds in common environmental components (c^2), but these differences are small.

Table IV. Genetic - (below the diagonal) and phenotypic* correlations (above the diagonal), heritabilities (on the diagonal) and common environmental components (c^2, on the last row) for Dutch Landrace (NL ♀) and Dutch Yorkshire (GY ♀ + ♂).

		UB	W/A	SC W	SC UB	INDEX
UB	NL	0.28±0.03	0.50	0.47	0.82	-0.20
	GY	0.23±0.02	0.56	0.53	0.89	-0.17
W/A	NL	0.25±0.07	0.12±0.02	1.00	0.06	0.73
	GY	0.48±0.06	0.18±0.02	0.99	0.24	0.71
SC W	NL	0.23±0.09	1.00±0.01	0.13±0.02	0.06	0.73
	GY	0.47±0.06	1.00±0.01	0.19±0.02	0.24	0.72
SC UB	NL	0.97±0.01	0.03±0.09	0.02±0.09	0.39±0.04	-0.64
	GY	0.96±0.01	0.24±0.08	0.24±0.08	0.27±0.03	-0.50
INDEX	NL	-0.70±0.15	0.52±0.07	0.53±0.07	-0.84±0.03	0.26±0.03
	GY	-0.37±0.07	0.64±0.05	0.64±0.05	-0.59±0.05	0.22±0.02
c^2	NL	0.20±0.01	0.22±0.01	0.23±0.01	0.17±0.01	0.21±0.01
	GY	0.21±0.01	0.21±0.01	0.20±0.01	0.21±0.01	0.19±0.01

*) All phenotypic correlations had a standard error < 0.01.

The size of the genetic and phenotypic correlations between W/A and SC W and between UB and SC UB were high as a result of autocorrelation. From a genetic point of view, W/A and SC W may be considered as identical traits. The correlations between SC W and SC UB were low (r_g = 0.02-0.24) whereas correlations of each of them with the index were high. There were differences between NL and GY for the correlations between backfat (UB or SC UB) and daily gain (W/A or SC W) and between the scores and INDEX. The differences in the genetic correlations were not significant, but some of the differences in phenotypic correlations were significant ($P < 0.01$), e.g. the correlation between SC W and SC UB.

DISCUSSION

Since the introduction of the on-farm test in The Netherlands, daily gain and backfat thickness phenotypically have improved considerably. If the average results in Table II are compared with the data used to construct the on-farm index (Minkema, 1973), W/A increased between 45 - 98 g/day, whereas UB decreased between 0.1 - 1.9 mm. Scores and index values also improved. The scores were constructed with an average of 0 and a standard deviation of 1, whereas the index was scaled on an average of 10 and a standard deviation of 2.5. In spite of a large improvement for both scores, a major reduction in variation appeared only for SC UB. Recently a recalculation of the parameters for the on-farm index resulted in minor changes in the regression coefficients, while the index value was rescaled on a standard deviation of 2.5 (Knap, 1986).

Season effects were statistically significant for each characteristic, but as also reported by Standal (1973), only a small part of the total variance was explained. The significant year x month interactions and their least squares means indicated that there was little consistency in the effect of season in the different years. Only for UB a slight tendency did appear for pigs born in April through September, and subsequently tested in October through February, to have thicker backfat while their weight was at a constant level. Significant year x season of test effects were also reported in on-farm or auction-test results by Hofstra and Minkema (1973), Harbeck (1981) and Sönnichsen (1983). Because of their size season effects are of low importance for the evaluation of on-farm test results (Standal, 1973). Nevertheless,

herd-year-season effects may be incorporated in models for genetic evaluation of on-farm test results to correct for environmental trend, as done by Hudson and Kennedy (1985).

The significance and the size of the herd effects agreed with results of Curran (1973), Standal (1973), Walters et al. (1977), Harbeck (1981), Scholling (1981) and Sönnichsen (1983). The intra-herd correlations (t) for backfat thickness are similar to those reported by Scholling (1981). For daily gain, t is somewhat larger. This difference for daily gain is probably due to the larger standard deviation in the data analysed, especially for GY ♂. The intra-herd correlations also agree well with the estimates of Hofstra and Minkema (1973). If compared with studies using dairy cattle, the differences between herds are smaller for daily gain and backfat thickness (t = 0.10 - 0.19) than for milk yield (t = 0.32-0.39; Haussmann, 1979). Nevertheless, a correction for herd effects in on-farm test data is to be recommended for across herds comparisons.

The differences between herds due to sire selection are small (h^2_{HS} = 0.0 - 0.2) within regions (Table III). This random use of sires is attributable to the intensive use of a limited number of AI-boars (since 1974) within each herdbook region. Across regions however, exchange of genetic stock has to arise from selling or buying potential AI and natural service boars. This causes a non-random use of sires indicated by the moderate h^2_{HS}-values (h^2_{HS} = 0.07 - 0.38) if no correction is made for region effects. If the genetic herd differences due to dam selection are equal to the differences due to sire selection (dependent on dam and sire selection in the past), two times h^2_{HS} may be an indication of total genetic herd differences. These total genetic differences are somewhat lower than the herd heritability (h^2_H) estimates of Standal (1973) h^2_H = 0.38 and Scholling et al. (1981) h^2_H = 0.0 - 0.7; probably the result of the intensive use of AI in the Dutch herdbook breeding programme. For across herds comparisons the reported herd differences due to sire selection make a correction for genetic herd differences necessary.

In the data analysed herds were almost fully nested within inspectors. If this is a stable situation, it is not necessary to have a correction for inspector effects as long as herd effects are included in the evaluation of on-farm test results. If each herd will be supervised by more than one inspector, however, the size of inspector effects will be too large to ignore in the evaluation of on-farm test results.

The genetic parameters (Table IV) were estimated in a model with significant sire x herd interactions. Hofstra and Minkema (1973) included a non-significant interaction in their analysis of on-farm test results. Nevertheless, the heritabilities were very similar for NL in both studies. The size and the relevance of the sire x herd interaction will be discussed in the next paper of this series.

The heritabilities estimated for SC W (h^2 = 0.13-0.19) and SC UB (h^2 = 0.27-0.39) correspond to the estimates of Standal (1977), Scholling (1981), Harbeck (1981), Sönnichsen (1983) and Gueblez and Sellier (1986) in similar data. Curran (1973), Hamelin et al. (1976) and Walters et al. (1977) reported higher heritabilities for on-farm test results. However, these heritabilities were pooled within-farm estimates and, therefore, probably biased upwards because of confounding of genetic and herd effects (Hofstra and Minkema, 1973; Standal, 1977). Common environmental effects (c^2) were about 0.20, which is comparable to the estimates in the literature. The differences between NL and GY in heritabilities for SC W agreed with the breed difference for the same trait in central test results (Merks, 1986). Similar breed differences were also reported in French on-farm test data (Hamelin et al. 1976, Gueblez and Sellier, 1986).

The small to moderate positive genetic correlations between SC UB and SC W (r_g = 0.02-0.24) agreed with results of Curran (1973), Standal (1977), Walters et al. (1977), Hamelin et al. (1976), Scholling (1981) and Sönnichsen (1983). The breed difference for these correlations, lower (genetic) correlations for the Landrace, is also reported by Walters et al. (1977), Hamelin et al. (1976) and Gueblez and Sellier (1986). The same difference was found in Dutch central test results (Merks, 1987). Hofstra and Minkema (1973) reported for NL a higher genetic correlation between SC W and SC UB (r_g = 0.36) than estimated in this study. The change in this correlation might be due to selection, as each trait improved phenotypically considerable.

The genetic parameters obtained in this study were, like others derived from field populations, biased by selection (Sorensen and Kennedy, 1984). Some bias may come from preselection of candidates for performance testing. The effects of the initial selection at about 25 kg were not large in a subset of each breed (Van Ham and Merks, 1986). As farmers are not obliged to test all their boars and gilts, they may select among the pigs that are eligible for the on-farm test. This selection probably would also bias heritability esti-

mates, but the size of this preselection is unknown. Paternal half sib estimates of genetic variances are biased with respect to the variance among chosen sires. The sires used were almost all central tested AI-boars with the same selection intensities as reported for the sires of central tested pigs (Merks, 1986). This may have reduced the genetic variance by 10 to 20 percent (Robertson, 1977).

The low genetic correlation between SC W and SC UB allows a genetic evaluation programme for each trait in a single trait model as suggested by Hudson and Kennedy (1985). Such an evaluation might include an appropriate correction for the environmental effects reported in this study, and genetic herd differences might be taken into account by use of the relationship-matrix. Such a mixed-model evaluation would enable an unbiased comparison of on-farm test results across herds. To have immediate access to the on-farm test results, a herdmate comparison procedure (Henderson et al., 1954) might be used.

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CHAPTER 4

SIRE X HERD INTERACTION IN ON-FARM TEST RESULTS

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ABSTRACT

On-farm test records from 31268 Dutch Landrace (NL) gilts, 11169 Dutch Yorkshire (GY) gilts and 16828 GY boars were used to examine sire x herd interactions. Sire x herd interactions were significant ($P < 0.001$) for all on-farm test characteristics in each of the three data sets. The interaction effect explained 11 to 23 % of the variance, depending on the characteristic. The genetic correlations between sires' progeny in different herds varied between 0.3 and 0.7 for weight corrected for age and between 0.6 and 0.9 for backfat thickness corrected for weight. The intra-class correlations, derived from the components of variance for sire and sire x herd effects, were somewhat higher than the average weighted genetic correlations between sires' progeny for each pair of herds.

Nonrandom mating, preferential treatment of pigs and environment-specific genes are discussed as possible causes of the sire x herd interactions. As the differences in environment between herds are numerous and sometimes undefinable, selection of sires on basis of sibs or even progeny results in different herds becomes attractive. Indications for sire x sex interaction were derived from the genetic correlations of 0.9 for weight corrected for age and 0.85 for backfat thickness corrected for weight between male and female progeny of GY-sires.

INTRODUCTION

The existence of genotype x environment interaction (G x E) in pig breeding programmes, has been derived from poor genetic relationships between similar traits measured in different levels of the breeding programme (e.g. Standal, 1977; Bampton et al., 1977; Groeneveld et al., 1984; Ollivier et al., 1984). These poor relationships may be the result of interactions between genotype and factors such as feeding regimen and housing system (Webb and Curran, 1986). But in a breeding programme with several herds within a level of the breeding programme and sires used across herds, G x E may be present also as a sire x herd interaction. This kind of interaction, represented by the genetic correlation among various herds r_g as described by Merks (1986), may be responsible for interaction of genotype and level of the breeding

programme (represented by r_G). Since r_g gives a type of upper limit for r_G (Brascamp et al., 1985), estimates of r_g in particular will contribute to a better understanding of the G x E problem in pig breeding programmes.

In an earlier paper of this series (Merks, 1987) the existence of sire x herd interaction was reported in the multiplication level for on-farm test results. In this paper the significance of this sire x herd interaction is investigated and the genetic correlations among identical traits measured in various herds are estimated.

MATERIAL AND METHODS

The data used were from Dutch Landrace (NL) gilts and Dutch Yorkshire (GY) gilts and boars tested in the herdbook field testing programme between May 1980 and December 1983 and were described previously by Merks (1987). In the on-farm test, pigs are weighed and their backfat thickness is measured ultrasonically at about 190 days of age. A performance index is calculated on the basis of age (AGE), weight (WEIGHT) and backfat thickness (UB). This index (INDEX) is a linear combination of two scores; a score for weight corrected for age (SC W) and a score for backfat thickness corrected for weight (SC UB). The corrections are performed with the average within animal regression of weight on age and backfat thickness on weight as estimated by Minkema (1973) from experimental data.

To investigate the significance of the sire x herd interaction for the different characteristics, least squares analyses were performed according to model 1 with the LSML76 programme (Harvey, 1977). The respective numbers of sire x herd cells for NL♀, GY♀ and GY♂ were 2750, 2021 and 1961 with averages of 11.4, 5.5 and 8.6 pigs per cell. The data were precorrected with the least squares means for month x year classes as described by Merks (1987).

$$y_{hijkl} = \mu + YB_h + \underline{S}_{i:h} + H_j + \underline{S \times H}_{ij} + \underline{D}_{k:ij} + \underline{e}_{ijkl} \qquad \text{(model 1)}$$

where,

$\underline{y}_{hijkl}$ = the record of the l-th animal
YB_h = the (fixed) effect of the year of birth h
$\underline{S}_{i:h}$ = the (random) effect of sire i with variance σ^2_S
H_j = the (fixed) effect of herd j
$\underline{S \times H}_{ij}$ = the (random) interaction effect of sire i and herd j with variance σ^2_{SH}
$\underline{D}_{k:ij}$ = the (random) effect of the k-th litter within the ij-th sire x herd class with variance σ^2_D
$\underline{e}_{ijkl}$ = residual error with variance σ^2_e

The coefficients of determination ($R^2(SH)$) were calculated for the interaction effect according to (1). The notation of Searle (1971) was followed for the reduction in sums of squares.

$$R^2(SH) = \frac{R(SxH|\mu,S,H)}{y'y - R(\mu)} \times 100 \qquad (1)$$

Sire x herd interaction can be represented by r_g, the genetic correlation among identical traits measured in various herds. The suggestion of Brascamp et al. (1985) was followed to estimate r_g. For each pair of herds r_g was derived from the correlation between breeding values of sires with progeny in both herds. The many pairwise estimates of r_g were pooled. Breeding values for SC W, SC UB and INDEX were estimated within herds by means of the univariate full sib REML-programme of Meyer (1987). Model 1 without year of birth of the sires, herd and interaction effect was followed. UB and weight for age (W/A) data were not used for these analyses as they were not corrected for variation in weight and age respectively and were genetically identical to SC UB and SC W (Merks, 1987). Covariances between $\underline{S}$, $\underline{D}$ and $\underline{e}$ have been assumed to be absent.

The computing strategy, described by Meyer (1987), uses an iterative procedure. Herewith the variance components estimated according to model 1 in the whole data set, are used as priors. The iterative procedure was stopped for each herd as soon as the change in the sire variance was less than 0.01 %. Convergence was reached for most herds within 25 rounds of iteration. Only for a few herds, in which the sire variance approached zero, convergence was not

reached within 100 rounds of iteration. For these herds the sire variance component was set to zero and breeding values were not estimated.

The genetic correlation among identical traits measured in various herds was derived from the correlations between breeding values for each pair of herds. The correlation between the breeding values of s sires in herd 1 with the breeding values of the same sires in herd 2 ($r_{\hat{A}1\hat{A}2}$), is according to Blanchard et al. (1983), related to the genetic correlation (r_g) as follows:

$$r_g = \sqrt{\frac{\sum_i b_{i1} \sum_i b_{i2}}{\sum_i b_{i1} b_{i2}}} * r_{\hat{A}1\hat{A}2} \qquad (2)$$

where $i = 1, \ldots s$ and b_{ij} $(j = 1,2)$ is the regression of half the breeding value of sire i on the progeny average y_{ij} in herd j according to:

$$b_{ij} = \frac{0.25\ h^2 nm}{1 + 0.25h^2\ (n(m+1)-2) + c^2(n-1)} \qquad (3)$$

where,

m = number of litters of sire i in herd j

n = average number of pigs per litter of sire i in herd j

h^2 = heritability of the trait

c^2 = common environmental effect of littermates.

Within-herd estimates of genetic parameters were used for the regressions. For this, analyses of variances with sires and litters nested within herds were performed. The many pairwise estimates of $r_{\hat{A}1\hat{A}2}$ and r_g were pooled by weighting the separate estimates by the number of sires with progeny in both herds as done by Bertrand et al. (1985). Only pairs of herds were used with at least 3 sires in common and for each sire at least two litters per herd.

The genetic correlation among herds also was estimated by the intra-class method (Dickerson, 1962; Yamada, 1962) from the components of variance for sires (σ^2_S) and for the interaction effect (σ^2_{SH}) estimated in model 1:

$$r_g = \frac{\sigma^2_S}{\sigma^2_S + \sigma^2_{SH} - var(\hat{\sigma}_{S_j})} \qquad (4)$$

where var ($\hat{\sigma}_{S_j}$) represents the variance of the genetic scale among environments. It has been shown by Fernando et al. (1984) that this estimate of r_g is biased if data are unbalanced or if the residual or sire variances are unequal across environments. Nevertheless, the method still has some merit due to its ease of computation, and the bias may be relatively small compared to the bias introduced in the pooled genetic correlation by means of the approximate relationship between $r_{\hat{A}1\hat{A}2}$ and r_g. Var ($\hat{\sigma}_{S_j}$) was obtained by calculating the variance of the sire standard deviations which were estimated simultaneously with the within herd breeding values. For the intra-class correlations lower bound estimates of the standard errors were obtained as done by Merks (1986). Herewith the standard errors of var ($\hat{\sigma}_{S_j}$) were not taken into account.

The size of sire x sex interactions was also investigated. Best linear unbiased predictions of breeding values for sires of GY-boars ($\hat{A}_m$) and GY-gilts ($\hat{A}_f$) were obtained by the computing algorithm of Schaeffer and Kennedy (1986) according to model 2. For sires with progeny in both data sets, correlations between breeding values were computed and the approximate relationship between $r_{g_{mf}}$ and $r_{\hat{A}_m\hat{A}_f}$ (formula 2 and 3) was used to estimate $r_{g_{mf}}$.

$$\underline{y}_{ijk} = HYS_i + \underline{L}_{j:i} + \underline{a}_{k:ij} + \underline{e}_{ijk} \qquad \text{(model 2)}$$

where,

HYS_i = the (fixed) effect of the i-th herd-year-season
$\underline{L}_{j:i}$ = the (random) effect of the j-th litter within the i-th HYS
$\underline{a}_{k:ij}$ = the (random) additive genetic effect of the k-th pig in the ij-th litter
$\underline{e}_{ijk}$ = random error.

Variances of litters, pigs and residuals (σ^2_L, σ^2_a and σ^2_e) have been assumed constant over all i, j and k. Covariances among $\underline{a}_{ijk}$ were included as numerator relationships among pigs; all other covariances among random elements of the model have been assumed to be zero. Seasons were defined from March through September and from October through February (Merks, 1987). The computing strategy, described by Schaeffer and Kennedy (1986), uses an iterative procedure which was stopped when the average absolute change in animal solutions was less than 0.1 % of one standard deviation of animal solutions.

RESULTS

The sire x herd interaction was significant ($P < 0.001$) for all traits in each of the three data sets. Coefficients of determination ($R^2(SH)$) showed a large contribution of the interaction effect to the total variance (Table I). The variance components for the interaction effect are in general larger or of the same size as the sire variance components, except for UB and SC UB.

Table I. Coefficients of determination for the sire x herd interaction ($R^2(SH)$) and variance components for interaction and sire effects.

	NL ♀			GY ♀			GY ♂		
	$R^2(SH)$	σ^2_{SH}	σ^2_S	$R^2(SH)$	σ^2_{SH}	σ^2_S	$R^2(SH)$	σ^2_{SH}	σ^2_S
UB	12.1	0.23	0.32	23.1	0.35	0.23	14.4	0.18	0.18
W/A	12.4	176	71	21.2	284	122	13.9	165	153
SC W	12.6	0.070	0.028	21.0	0.061	0.028	14.5	0.046	0.039
SC UB	11.4	0.025	0.069	21.7	0.046	0.039	14.7	0.029	0.027
INDEX	12.9	0.250	0.306	21.7	0.174	0.168	15.7	0.234	0.195

The sire x herd interaction component may be inflated by differences in genetic scale between environments. Heterogeneity of genetic variances was investigated by estimation of variance components within herds. The variance of the within-herd sire standard deviation is given in Table II for SC W, SC UB and INDEX. For these traits, an important part of the sire x herd variances

Table II. Variance components for the interaction and sire effect and the variance of sire variation within herds ($var(\hat{\sigma}_{S_j})$).

	NL ♀			GY ♀			GY ♂		
	σ^2_S	σ^2_{SH}	$var(\hat{\sigma}_{S_j})$	σ^2_S	σ^2_{SH}	$var(\hat{\sigma}_{S_j})$	σ^2_S	σ^2_{SH}	$var(\hat{\sigma}_{S_j})$
SC W	0.028	0.070	0.023	0.028	0.061	0.031	0.039	0.046	0.030
SC UB	0.069	0.025	0.019	0.039	0.046	0.022	0.027	0.029	0.026
INDEX	0.306	0.250	0.138	0.168	0.174	0.107	0.195	0.234	0.139

was due to unequal genetic variances in the different herds. This heterogeneity of genetic variances is only to a small extent related to the within herd standard deviation and even less to the herd mean (Table III).

Table III. Correlations of within herd sire standard deviations with herd means and within herd standard deviations.

	NL ♀		GY ♀		GY ♂	
	herd mean	herd s.d.	herd mean	herd s.d.	herd mean	herd s.d.
SC W	-0.19	0.42	0.22	0.47	0.29	0.37
SC UB	0.11	0.24	-0.21	0.11	0.19	0.43
INDEX	-0.24	0.38	0.09	0.44	0.15	0.23

The relevance of the sire x herd interaction for the breeding programme is measured by r_g, the genetic correlation among identical traits measured in different herds. For the calculation of the average weighted correlations, herds with little or no genetic variance ($\sigma^2_s \cong 0$) were left out. About 50 % of the possible pairs of herds with NL ♀ and about 65 % of the possible pairs with GY ♀ or GY ♂ had no or less than three sires in common. The number of pairs of herds with sires in common is given in Table IV along with the average number of common sires for these pairs and the genetic parameters used. The average weighted genetic correlations ranged between 0.28 and 0.72. The large standard deviations reflect the large variation in correlations between the different pairs of herds.

The variances in Table II were used to calculate the intra-class correlation between sires' progeny in different herds. The size of these correlations presented in Table V, is in the same range as the average weighted correlations (Table IV) but at a somewhat higher level. The standard errors tabulated are the lower bound estimates.

Table IV. Overall within-herd heritabilities (h^2) and common environmental effects (c^2) used to estimate the average weighted correlations between breeding values ($r_{\hat{A}i\hat{A}j}$) for n pairs of herds with an average of $\bar{s}$ sires in common and the average weighted genetic correlations among herds (r_g). (The standard deviations of the weighted estimates are between brackets.)

	NL ♀		GY ♀		GY ♂	
	h^2	c^2	h^2	c^2	h^2	c^2
SC W	0.47	0.15	0.51	0.13	0.45	0.16
SC UB	0.52	0.14	0.50	0.15	0.57	0.14
INDEX	0.49	0.15	0.38	0.19	0.48	0.16

	n = 1258 $\bar{s}$ = 15.2		n = 627 $\bar{s}$ = 12.7		n = 623 $\bar{s}$ = 10.1	
	$r_{\hat{A}i\hat{A}j}$	r_g	$r_{\hat{A}i\hat{A}j}$	r_g	$r_{\hat{A}i\hat{A}j}$	r_g
SC W	0.12(0.29)	0.28(0.77)	0.13(0.30)	0.38(0.97)	0.19(0.33)	0.50(0.98)
SC UB	0.32(0.27)	0.72(0.70)	0.17(0.29)	0.51(0.95)	0.24(0.33)	0.59(0.86)
INDEX	0.23(0.30)	0.52(0.78)	0.16(0.30)	0.57(1.19)	0.20(0.34)	0.53(0.99)

The sire x sex interaction was tested by correlating the breeding values of sires with progeny in the GY-boars and GY-gilts data. The correlations in Table VI indicate the presence of sire x sex interaction for the traits analysed.

Table V. Genetic correlations between sires' progeny in different herds estimated by $\sigma_S^2/[\sigma_S^2+\sigma_{SH}^2-\text{var}(\hat{G}_{S_j})]$ with their lower bound standard errors.

	NL ♀	GY ♀	GY ♂
SC W	0.37 ± 0.04	0.48 ± 0.06	0.71 ± 0.06
SC UB	0.92 ± 0.04	0.62 ± 0.06	0.90 ± 0.05
INDEX	0.73 ± 0.04	0.71 ± 0.08	0.67 ± 0.06

Table VI. Correlations between breeding values of GY-sires based on male and female progeny ($r_{\hat{A}_m\hat{A}_f}$) and the derived genetic correlations ($r_{g_{mf}}$).

	GY ♀ - GY ♂ (no. sires = 155)	
	$r_{\hat{A}_m\hat{A}_f}$	$r_{g_{mf}}$
SC W	0.67	0.90
SC UB	0.68	0.85
INDEX	0.60	0.78

DISCUSSION

The results showed a highly significant sire x herd interaction for all on-farm test characteristics. This interaction has not been reported previously in similar data, but probably only Hofstra and Minkema (1973) tested this sire x herd interaction. The absence of the interaction effect in statistical models used to analyse other on-farm test results (e.g. Groeneveld et al., 1984; Ollivier et al., 1984), might be due to the absence or limited use of AI. Without AI or intensive exchange of sires across herds, sire x herd interactions can not be tested. Significant sire x herd or sire x contemporary group interactions are also reported for birth weight and weaning weight in beef cattle field data (Burfening et al., 1982, Bertrand et al., 1985 and Bertrand et al., 1987).

The sire x herd variances tabulated in Table I are inflated by heterogeneity of genetic variances. The size of the inflation is determined by var ($\hat{\sigma}_{S_j}$) which turned out to be large, especially for SC UB. However, a correct evaluation of the size of inflation should take into account that var ($\hat{\sigma}_{S_j}$) is approximated; it is to be expected that var ($\hat{\sigma}_{S_j}$) $\geq$ var (σ_{S_j}) (Brascamp et al., 1985). The size of the within herd sire variance was not related to the herd level as has been reported for dairy cattle (e.g. Hill et al., 1983). This may be due to the moderate relationship between phenotypic and genetic heterogeneity (r = 0.11 to 0.47; Table III). From this follows that a correction for the heterogeneity of variances amond herds as suggested by Brotherstone and Hill (1986), will only be partly succesful in reducing the heterogeneity of the ge-

netic variances in on-farm test results. The suggestion of Gianola (1986) to tackle heterogeneous variances may be more effective, but the computations required for that will seldom be feasible for on-farm test results. Other solutions must be searched if this heterogeneity is due to differences between herds in preselection among test candidates for fitness-related traits (e.g. leg quality).

Two distinct procedures were used to estimate the genetic correlations among identical traits measured in various herds, but both estimation procedures have deficiencies. The pooled correlations across herds are obtained by an approximation of the relationship between breeding values and the genetic correlations, and the assumptions underlying this relationship (Taylor and Everett, 1982) might not be fullfilled. A part of the approximation concerns the genetic parameters used. A model with a nested design was used to estimate these parameters instead of separate estimates for each herd, to avoid extreme small or large values. However, the robust within-herd heritabilities are biased upwards if there is heterogeneity of within-herd variances. This heterogeneity being present, the genetic correlations reported in Table IV may be underestimated to an important extent. Use of the heritabilities estimated across herds (Merks, 1987), which were about half the size of the within-herd heritabilities, resulted in genetic correlations between 0.61 and 0.94. The estimation of r_g might be improved by using a two-trait model for each pair of herds - trait one measured in herd one, trait two measured in herd two - and estimating the genetic correlation for that pair of herds.

The adjusted intra-class estimate of the genetic correlation is biased due to the unbalancedness of the data as well as to unequal sire and error variances in the different herds (Fernando et al., 1984). Further, var ($\hat{\sigma}_{s_j}$) may be overestimated as referred to earlier.

Comparison of the two types of estimates shows that the intra-class correlations are 20 to 40 % higher than the pooled genetic correlations across herds. As the pooled correlations may be underestimated to an important extent, the intra-class correlations may be more reliable despite the fact that they are also biased. The estimated correlations point at a stronger sire x herd interaction for SC W than for SC UB; r_g = 0.3 - 0.7 for SC W and r_g = 0.6 - 0.9 for SC UB. For weaning weight of beef cattle comparable genetic correlations between sires' progeny across regions were obtained (r_g = 0.6 to 0.9; Bertrand et al., 1985, Bertrand et al., 1987).

In different studies of G x E in pig breeding programmes, genotype x sex interaction has been indicated as a possible cause for interaction across levels of the breeding programme (e.g. Standal, 1977; Ollivier et al., 1984). In this study the genetic correlation between male and female progeny of GY-sires ranged between 0.78 and 0.90 (Table VI). These indications for sire x sex interactions agree with similar findings reported in central test results (Merks, 1986). However, the two sexes were tested on partly different herds. This may have caused differences in environment and or treatment of the two sexes and consequently be the origin of the sire x sex interaction.

The use of aged coefficients (Minkema, 1973) to perform the corrections of weight for age and backfat thickness for weight might have arisen some of the sire x herd interactions. However, the use of the coefficients calculated by Knap (1986) appeared to have little or no effect on the genetic correlations and the relative size of the variance components. Two possible causes remain for the sire x herd interactions reported. The first cause could be an enhanced correlation among sire progeny groups in some herds due to nonrandom mating or preferential treatment of pigs. Indications of nonrandom mating in these data were found previously in genetic herd differences due to sire selection (Merks, 1987). Including female parents in a mixed model analysis should control problems associated with nonrandom mating. Bertrand et al. (1987) reported for weaning weight of beef cattle average weighted genetic correlations across regions before and after accounting for dams of 0.55 and 0.66 respectively. Preferential treatment of pigs may be found in scale feeding according to weight. Kanis (1987) reported litter x feeding regimen interactions when differences in feed intake capacity were not taken into account.

The second cause for sire x herd interactions might be biological; different sets of genes determine the expression of a trait in different environments. Since the differences between herds are numerous and sometimes undefinable (e.g. pathogen levels and management), it is very unlikely that only factors like feeding level or housing system are responsible for the sire x herd interactions. In that case selection of sires on basis of sib or even progeny results in different herds may be desirable. Brascamp et al. (1985) indicated that progeny testing becomes more attractive than the use of sib results in case the correlation between central test and on-farm test (indicated as r_G) is below 0.5. As the estimated correlations among herds are a type of upper

limit for r_G (Brascamp et al., 1985), at least for SC W progeny testing may be more efficient. However, the impact of G x E on the breeding programme depends not only on the genetic correlation among herds within on-farm testing. The other parameters and correlations that are needed, i.e. the genetic correlations among fattening herds and between the different levels of the breeding programme, will be reported in the subsequent papers.

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CHAPTER 5

GENETIC PARAMETERS AND SIRE X HERD INTERACTION IN COMMERCIAL FATTENING

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ABSTRACT

A progeny test of 107 Dutch Yorkshire AI-boars was set up under commercial fattening conditions to estimate genetic parameters and to examine sire x herd interactions under these conditions. Individual records of 8148 crossbred fattening pigs, born on 27 sow herds and fattened on 35 fattening herds were obtained. The information included daily gain during the fattening period (DGF) and during life (DGL), carcass weight (CW) and a score for backfat thickness (BC) and type (T).

Heritability estimates for DGF, DGL and CW were 0.05, 0.08 and 0.05 respectively for a model that included a significant sire x herd interaction, but somewhat higher if the interaction was excluded. For BC and T the sire x herd interaction was not significant ($P > 0.05$) and a heritability of 0.10 was estimated for both traits. The genetic correlations of CW with DGF and DGL were about one; the result of the "all in - all out" management at the fattening herds. Measurement of CW, as a simple but accurate indicator for daily gain, will facilitate a large scale progeny test.

Genetic correlations between sires' progeny in different herds, estimated from variance component estimates, were 0.29 for DGF and 0.52 for DGL. The average weighted genetic correlations between sires' progeny for each pair of herds were somewhat lower. Non-random mating and preferential treatment are not likely to contribute to the sire x herd interaction in commercial fattening. As there are so many environmental differences between commercial herds, environment-specific genes are expected to be responsible for the low genetic correlations among herds.

INTRODUCTION

In pig breeding programmes with different levels, e.g. nucleus herds with testing at central stations, multiplication herds with on-farm testing and commercial herds with fattening pigs, interaction of sire with level of the breeding programme lowers the potential efficiency of the breeding programme (Merks, 1986). Whether in that case testing of individuals, sibs or progeny in multiplication or commercial fattening herds is more efficient than testing in a test environment depends on several factors. Next to intensity of selection

and generation interval, heritabilities of the traits measured under commercial conditions, the genetic correlation among commercial environments (represented by r_g) and the genetic correlation between levels of the breeding programme (represented by r_c; Merks, 1986) are important.

In several studies heritabilities for on-farm test characteristics were reported, but the genetic correlations among herds for on-farm test data were reported only by Merks (1987c). The genetic correlations between sires' progeny in different herds ranged from 0.3 to 0.9; a result of significant sire x herd interactions. For traits measured on commercial fattening herds only a few heritability estimates are available (McGloughlin, 1977; Ketelaars, 1979 and Claus et al., 1984), while no estimates of the genetic correlations among commercial fattening herds are reported in literature. Therefore a progeny test of AI-boars was set up under commercial fattening conditions. The boars used had a performance record in central test or on-farm test. In this paper genetic parameters and genetic correlations between sires' progeny in different herds were estimated for the fattening and carcass characteristics measured on the commercial fattening herds. The genetic correlations between central test, on farm test and commercial fattening will be reported in a subsequent paper.

MATERIALS AND METHODS

A progeny test of young Dutch Yorkshire (GY) AI-boars was set up in co-operation with 27 commercial sow herds, a co-operative AI-centre and a co-operative slaughterhouse. All boars purchased by the AI-centre between July 1982 and July 1984, both central-tested (CT) and on-farm tested (FT), were available for the experiment. The CT boars were selected on conformation, own-performance and on sib results for fattening and carcass characteristics (Merks, 1986). The FT boars were selected on conformation and performance for daily gain and backfat thickness (Van Kemenade, 1987).

The AI-boars were used at random across the 27 sows herds between November 1982 and November 1984. From each boar a maximum of 150 inseminations was allowed. The goal was to have 100 inseminations per sire which would result in about 30 registered litters each with at least three slaughtered and recorded pigs. This number of progeny per sire would enable accurate estimation of the sires' breeding value, even for traits with a rather low heritability. At the

participating sow herds all piglets were identified with individual metal ear clips before weaning and the identification numbers were recorded together with sire, litter, dam's breed type and date of birth. At the time the piglets left the sow herd to go to the fattening herds, they were registered and weighed. About half of the sow herds had their own fattening unit in which the major part of their pigs was fattened. The other pigs were fattened in additional herds. At the end of the fattening period the pigs were slaughtered at a normal slaughter weight of about 105 kg live weight. In the slaughterhouse every pig passed a post mortem evaluation where the carcass weight was measured and a carcass classification according to EEC-regulations was performed (De Boer, 1982). Pigs were identified at the slaughterhouse by their individual ear numbers.

After the last pigs were slaughtered (November 1985), the data were screened for carcass weight and age at slaughtering. Only records with a carcass weight between 50 and 110 kg and an age at slaughtering between 135 and 250 days were selected. After screening, data remained from 35 fattening herds. Table I shows the number of sires with their progeny used in the analyses as well as the number of pigs for each breed type of the dam. Per sire in average 24.4 litters, each with 3.1 pigs, were recorded.

Table I. Numbers of central-tested (CT) and on-farm-tested (FT) sires with numbers of progeny and the number of progeny for each breed type of the dam used in the analyses.

Sires		Progeny	Dam's breed type	Progeny
CT	65	4889	Dutch Yorkshire (GY)	49
FT	42	3259	Dutch Landrace (NL)	144
	107	8148	Duroc x NL	2199
			Finnish Landrace x NL	241
			GY x NL	4166
			Unknown	1349
				8148

Two traits of growth were considered; daily gain during the fattening pe-

riod (DGF) and the daily gain during life (DGL). Daily gain in the fattening period was calculated from the starting weight at the commercial fattening herd and the estimated live weight at slaughter (carcass weight multiplied by 1.3). The live weight gain (DGL) was calculated as estimated live weight at slaughter divided by the age at slaughtering. The carcass classification was decomposed into a score for backfat thickness (BC) and a score for type (T) as done in the analysis of central test results (Merks, 1986). The backfat thickness classes E, I, II and III were analysed as 1, 2, 3 and 4 respectively. Type classes AA, A, B and C were transformed into 3, 2, 1 and 0 respectively.

A large difference between commercial fattening and central or on-farm test may be found in the way pigs are grouped and in the end point of the growing period. Pigs are almost continuously entering central or on-farm test and tested as contemporaries over a certain weight or age interval. However, in commercial fattening groups of 80 - 120 pigs enter the fattening unit at the same time. They have about the same starting weight but they vary largely in age. These pigs are all slaughtered in 1 or 2 groups at a weekly interval. Due to this "all in - all out" management variation in carcass weight (CW) may partly be of genetic origin as indicated by McGlouglin (1977) and a simple indicator of daily gain during the fattening period. Consequently, the growth traits were not adjusted for the variation in CW, but CW was analysed as a separate trait.

Variances and covariances have been estimated according to model 1 by "Henderson's method 3" as programmed by Harvey (1977). The effects of sow herds were not included in the model as fattening herds were nested within these herds. In preliminary analyses the dam's breed type x herd interaction appeared to be not significant ($P > 0.05$) and was therefore excluded from further analyses. Month of arrival at the fattening herd was chosen instead of month in which the pig was slaughtered for seasonal effects, in order to avoid confounding of seasonal and genetic effects. The number of sire x herd cells was 725 with on average 11.2 pigs per cell.

$$y_{ijklmno} = \mu + \underline{S}_i + H_j + \underline{SxH}_{ij} + B_k + M_l + Y_m + MxY_{lm} + \underline{D}_{n:ijklm} + \underline{e}_{ijklmno} \quad \text{(model 1)}$$

where

$y_{ijklmno}$ = the record of the o-th animal

$\underline{S}_i$ = the (random) effect of the i-th sire with variance σ^2_S

H_j - the (fixed) effect of the j-th fattening herd

$\underline{SxH}_{ij}$ - the (random) interaction effect of the i-th sire and the j-th herd with variance σ^2_{SH}

B_k = the (fixed) effect of the k-th breed type of the dam

M_l = the (fixed) effect of the l-th month of arrival at the fattening herd

Y_m - the (fixed) effect of the m-th year of arrival at the fattening herd

MxY_{lm} - the (fixed) effect of the interaction between month l and year m

$\underline{D}_{n:ijklm}$ - the (random) effect of the n-th litter with variance σ^2_D

$\underline{e}_{ijklmno}$ - residual error with variance σ^2_e

A second model, model 1 without the sire x herd interaction was used (Model 2) to study the effect of the sire x herd interaction on the estimation of genetic parameters. Because of possible differences in heritabilities for groups of sires, model 1 was also used to estimate the genetic parameters within the subsets of progeny of CT and FT sires.

The genetic parameters, heritabilities (h^2), common environmental components (c^2), genetic correlations between traits and their standard errors were estimated as in earlier analyses (Merks, 1986). For the proportion of variance explained by the interaction effect, the coefficients of determination (R^2 (SH)) were calculated according (1). The notation of Searle (1971) was followed for the reduction in sums of squares

$$R^2(SH) = \frac{R(SxH|\mu,S,H)}{y'y - R(\mu)} \times 100 \qquad (1)$$

The genetic correlations between sires' progeny in different herds were estimated (1) as the average weighted genetic correlation between sires' progeny for each pair of herds and (2) derived from the components of variance for sire and sire x herd effects as the intra-class correlation (Dickerson, 1962; Yamada, 1962). The procedures used to calculate these correlations were the same as applied to on-farm test data (Merks, 1987c). For the calculation of the weighted correlations between breeding values for each pair of herds, only pairs of herds were used with at least 3 sires in common and for each sire at least two litters per herd. The remaining 166 pairs of herds had in average

12.7 sires in common. For the approximate relationship between the genetic correlation (r_g) and the correlation between breeding values in each pair of herds ($r_{\hat{A}1\hat{A}2}$), the within herd genetic parameters were used. These genetic parameters were estimated according to a model with sires and litters nested within herds.

RESULTS

The average values and standard deviations of the traits analysed are given in Table II. The average age at slaughtering was 179 days, while the average number of days that the pigs were in the fattening pens was 110 days. The frequencies of the backfat thickness classes E, I, II and III were 16.6, 78.7, 4.6 and 0.1 % respectively. For type the frequencies for the classes AA, A, B and C were respectively 16.6, 69.5, 13.9 and 0.02 %.

Table II. Averages and standard deviations (S.D.) of the traits analysed.

Trait		Average	S.D.
Daily gain fattening period (g)	DGF	758.9	118.7
Daily gain live period (g)	DGL	596.1	71.0
Carcass weight (kg)	CW	82.7	7.1
Backfat thickness score	BC	1.88	0.45
Type score	T	1.97	0.55

The analyses of variance according to model 1 resulted in significant ($P < 0.001$) sire, litter and herd effects for all traits. The sire x herd interaction was significant for the growth traits and for CW ($P < 0.001$) but not ($P > 0.05$) for BC and T. The interaction effect explained a high percentage of the total variance (R^2(SH)) for the growth traits and CW (DGF 14.9 %; DGL 13.0 %; CW 13.2 %). Dam's breed type was significant for all traits ($P < 0.05$ for DGF, DGL and CW; $P < 0.001$ for BC and T). The month x year interaction was significant for the growth traits and CW ($P < 0.001$) but not for BC and T.

Genetic parameters were estimated according to the model with sire x herd

interaction (model 1) and a model without this interaction (model 2). The estimated parameters for both models are given in Table III. Differences in genetic parameters between the two models are only of importance for the heritabilities and common environmental components for DGF and DGL. Neglection of the sire x herd interaction for these traits resulted in higher estimates for heritabilities and common environmental components. Genetic variance was also present for carcass weight (h^2 = 0.05). The correlations of CW with the growth traits showed a close relationship.

Table III. Genetic (below the diagnonal) and phenotypic* correlations (above the diagonal), heritabilities (on the diagonal) and common environmental components (c^2, on the bottom two rows), estimated with (1) or without (2) sire x herd interaction in the model.

		DGF	DGL	CW	BC	T
DGF	1	0.05 ± 0.03	0.95	0.77	0.09	-0.07
	2	0.11 ± 0.03	0.94	0.77	0.09	-0.07
DGL	1	0.97 ± 0.06	0.08 ± 0.03	0.82	0.08	-0.06
	2	0.91 ± 0.03	0.11 ± 0.03	0.82	0.08	-0.06
CW	1	1.38 ± 0.28	1.21 ± 0.15	0.05 ± 0.03	0.05	-0.04
	2	0.93 ± 0.07	0.94 ± 0.06	0.06 ± 0.02	0.05	-0.04
BC	1	0.14 ± 0.29	0.12 ± 0.23	0.22 ± 0.26	0.10 ± 0.02	-0.73
	2	0.14 ± 0.19	0.15 ± 0.18	0.20 ± 0.21	0.09 ± 0.02	-0.73
T	1	-0.05 ± 0.29	-0.14 ± 0.23	-0.17 ± 0.27	-0.94 ± 0.04	0.10 ± 0.02
	2	-0.11 ± 0.19	-0.15 ± 0.18	-0.16 ± 0.21	-0.96 ± 0.04	0.09 ± 0.02
c^2	1	0.18 ± 0.02	0.18 ± 0.02	0.14 ± 0.02	0.05 ± 0.01	0.04 ± 0.01
	2	0.23 ± 0.02	0.21 ± 0.02	0.16 ± 0.01	0.05 ± 0.01	0.05 ± 0.01

The heritability estimates for the two groups of sires (central tested CT and on-farm tested sires FT) were similar; for DGF and T about equal to the overall estimates in Table III. The heritabilities for DGL and BC were respectively 0.09 ± 0.05 and 0.07 ± 0.03 for CT-sires and respectively 0.04 ± 0.05 and 0.13 ± 0.05 for FT-sires. Also the common environmental components and the correlations were for both groups of sires similar to those reported in Table III. In both data sets the sire x herd interaction was significant for DGF, DGL and CW but not for BC and T.

The relevance of the sire x herd interaction for the breeding programme is measured by r_g, the genetic correlation among identical traits measured in various herds. No estimates were made for the carcass characteristics as the sire x herd interaction was not significant for these traits. The average weighted genetic correlations for DGF and DGL are reported in Table IV together with the within herd genetic parameters used to calculate these correlations. The genetic correlations were low especially for DGF.

The intra-class correlations between sires' progeny in different herds are also tabulated in Table IV together with the variance components from which these correlations were estimated. The intra-class correlations were somewhat higher than the average weighted genetic correlations among herds. The standard errors tabulated are lower bound estimates.

Table IV. The average weighted correlations between breeding values ($r_{\hat{A}i\hat{A}j}$) and the average weighted genetic correlations among herds (r_{g_w}; the standard deviations of the weighted estimates are between brackets) with the used within herd heritabilities (h^2) and common environmental effects (c^2), and the intraclass correlations (r_{g_t}; ± lower bound standard errors) with the used variance components.

	h^2	c^2	$r_{\hat{A}i\hat{A}j}$	r_{g_w}
DGF	0.38	0.13	0.04 (0.30)	0.12 (1.18)
DGL	0.31	0.16	0.08 (0.31)	0.32 (1.40)

	σ^2_S	σ^2_{SH}	$var(\delta_{S_j})$	r_{g_t}
DGF	130	812	499	0.29 ± 0.11
DGL	78	174	102	0.52 ± 0.14

DISCUSSION

The data collected showed somewhat better results than the average results of the recorded fattening herds in the province where the progeny test was performed. In 1983 and 1984 these herds realised on average 673 g/day for DGF and 75 % of the carcasses classified EAA or 1A (Arkes et al., 1985), while the

average results in this study were 759 g/day and 83 % EAA + 1A. Individual herd averages indicated that the progeny test was performed on a group of herds with an above average management.

In all analyses the herd effect was significant ($P < 0.001$). Significant herd effects were also reported by McGloughlin (1977), Ketelaars (1979) and Claus et al (1984) for daily gain and backfat thickness in progeny data collected under field conditions. McGloughlin (1977) and Ketelaars (1979) reported a significant effect of the breed type of the dam on daily gain and type, which agrees with the results in this study. The absence of a significant sire x herd interaction for BC and T is not in agreement with the sire x herd interaction reported for backfat thickness in on-farm test results (Merks, 1987c). However, BC and ultrasonic backfat thickness are genetically not identical ($r_g = 0.42$; Merks, 1986), which makes this comparison less valid.

The heritabilities for DGF and DGL were affected by the sire x herd interaction. Excluding the interaction effect from the model would have given biased estimates for h^2 and c^2 as indicated by Latrope et al. (1984). The heritabilities estimated are comparable to the estimates of Ketelaars (1979) in commercial fattening results; DGF:h^2=0.08, BC:h^2=0.05-0.11, T:h^2=0.13-0.20. McGloughlin (1977) and Claus et al. (1984) reported somewhat higher heritabilities for daily gain (h^2 = 0.25 and h^2 = 0.28 respectively) and carcass backfat thickness (h^2 = 0.19 and h^2 = 0.12) measured under field conditions. However, these heritabilities were obtained without a litter effect in the model or as pooled within-farm estimates and are, therefore, probably biased upwards. The genetic correlations between DGF and DGL and between BC and T are similar to the correlations between the same traits measured on central tested pigs (Merks, 1986). The genetic correlations between DGF, BC and T are in the same range as the correlations reported by Ketelaars (1979). The large environmental variation in commercial fattening environment is probably the main reason for the relatively low heritabilities; that is also why central test units were set up in the past. Also the absence of a correction for the sex effects - the sex of the pig was not recorded - increased the environmental variance. For BC and T the small number of classes and classes being inconsistent with an underlying normal distribution may have contributed to the low heritabilities.

The heritability for CW was equal to that for DGF. The genetic correlations

of CW with DGF and DGL show, despite variation in age at slaughtering, a close relationship. This is due to the "all in - all out" management at the fattening herds. Correction of the growth traits for the variation in slaughter weight should therefore not be performed. Furthermore, for the investigated fattening system these results show that CW is an accurate measurement to record growth rate during the fattening period or during life. Because of the ease at which CW may be obtained, the set up of a large scale progeny test on fattening herds becomes less complicated.

The data analysed were almost all from crossbred pigs. Characteristic for crossbred animals is that part of the gene effects that appear non-additive in pure breeding act additively in the crossbreds (Falconer, 1983). Whether this has affected the genetic parameters estimated is unknown, but Standal (1968) and McLaren et al. (1985) reported that heritability estimates for post-weaning daily gain and backfat thickness were similar based upon either pure-bred or crossbred progeny.

The genetic parameters obtained in this study were, like others derived from field populations, biased due to selection of sires. The CT sires were selected with the same intensity as reported for sires of central tested pigs (Van Balkom, 1984; i = 0.68 for daily gain). The FT sires were progeny of central tested sires, and selected on basis of on-farm test with about the intensity as used for CT sires. The procedure of Robertson (1977) was applied to quantify the reduction in genetic variance and heritabilities. The calculated bias due to selection of sires was small because of the low heritabilities.

The relevance of the sire x herd interaction is measured by the genetic correlation between identical traits measured in two herds chosen at random. The average weighted genetic correlations among herds were somewhat lower than the intraclass correlations. This tendency was also present in the estimates of on-farm test data (Merks, 1987c), probably the result of an overestimation of the within-herd heritabilities. For both BC and T a genetic correlation of one may be assumed because sire x herd interaction is absent for these traits. An exact estimate of the genetic correlations for DGF and DGL may not be derived from the estimates in this study; both estimation procedures used have their deficiencies. The DGL correlations are similar to the genetic correlations reported for weight corrected for age in on-farm test data (Merks, 1987 c). The differences between DGF (r_g = 0.12 - 0.29) and DGL (r_g = 0.32 - 0.52) may be due to differences in intervals across which these traits were calcu-

lated. Both traits have the same end point; slaughter weight, but the starting point is a fixed birth weight for DGL and the weight at which the pig entered the fattening unit for DGF. An inaccuracy in the starting weight for DGL is to be expected as most weights were recorded as the average of the group. This source of variation seems to have more effect on the sire x herd interaction than the fact that DGL included daily gain during rearing, which in most cases was measured in another herd.

For on-farm test results different causes were suggested for the sire x herd interactions; non-random mating, preferential treatment and environment-specific genes (Merks, 1987c). For commercial fattening results non-random mating can not be a cause as the herdsmen could not choose a particular boar. Also the existence of preferential treatment is not likely in commercial fattening. Therefore, the cause for the sire x herd interaction must be biological here; different sets of genes that determine the expression of a trait in different environments. It is of importance to specify the relevant environmental factors, but as there are so many environmental differences between fattening herds, it is doubtful whether that will be possible.

From this study the possibilities as well as the limitations of a progeny test under commercial conditions may be derived. Genetic variance was present but the heritabilities were low compared to the heritabilities for similar traits measured in central or on-farm test (Merks, 1987a, 1987b). Also, the low genetic correlations between sires' progeny performance in different herds have a negative impact on the efficiency of a progeny test. On the other hand carcass weight seems to be a simple but accurate measurement of daily gain and therefore will facilitate a large scale progeny test.

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CHAPTER 6

GENETIC RELATIONS BETWEEN PERFORMANCES IN CENTRAL TEST, ON-FARM TEST AND COMMERCIAL FATTENING

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ABSTRACT

Data of the Dutch herdbook breeding programme and data obtained in a progeny test of AI-boars under commercial fattening conditions were used to calculate the genetic correlations between similar traits measured in central test, on-farm test and commercial fattening. The genetic correlations were derived from the correlations between best linear unbiased predictions of breeding values in the different environments.

A moderate genetic relationship was calculated between central and on-farm test; for backfat thickness r_{G1} = 0.3 - 0.7, for daily gain r_{G1} = 0.3 - 0.65. Differences in definition of the traits and differences in sex of the progeny groups were only partly responsible for the moderate relationships. For identical traits measured in central and on-farm test on progeny of the same sex r_{G1} = 0.41 for daily gain and r_{G1} = 0.70 for backfat thickness. Sire x herd interaction in on-farm test data was found to be the responsible factor for the moderate correlations between central and on-farm test.

Between progeny results in commercial fattening and performances of the sires in central test no clear relationship was found for daily gain, r_{G2} = -0.48 - 0.17, but high correlations for identical carcass characteristics, r_{G2} = 0.57 - 0.64. These results agreed closely with the presence of sire x herd interactions in commercial fattening for only daily gain.

The genetic correlations between on-farm test and commercial fattening were high for daily gain, $r_{G3} \cong 1.0$, but low for carcass characteristics, $r_{G3} \cong 0$. The presence of sire x herd interaction in both levels of the breeding programme may be responsible for the differences in correlations. It was concluded that the sire x herd interaction in on-farm test and commercial fattening results is the main factor responsible for the moderate genetic correlations between the different levels of the breeding programme.

INTRODUCTION

A profound description of genotype x environment interaction (G x E) in pig breeding programmes is given by Merks, (1986). Three levels were distinguished; nucleus herds with testing at central stations, multiplication herds with on-farm testing and commercial herds with fattening pigs. The impact of

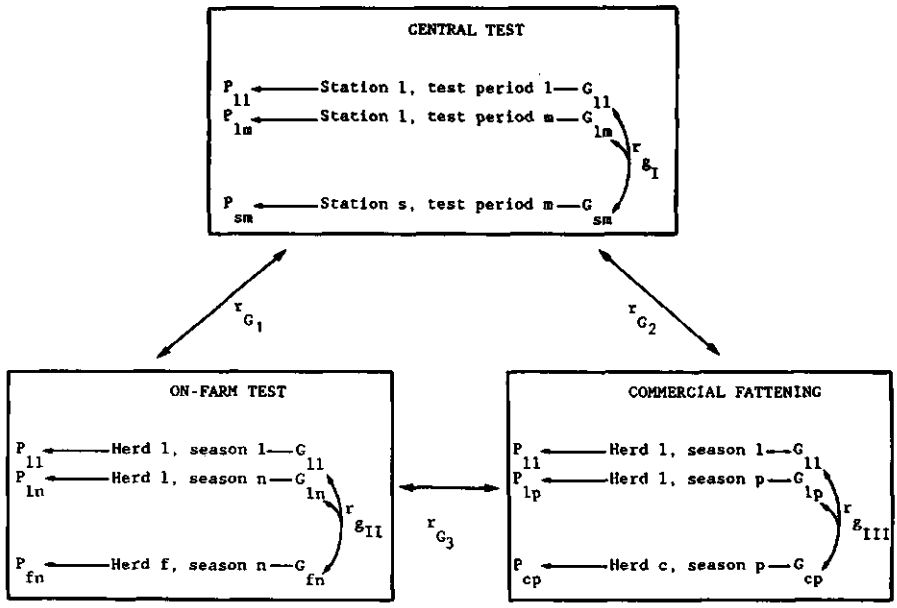

Figure 1. Schematic description of the genotype x environment interaction problem in pig breeding programmes.

G x E on the breeding programme was interpreted as (1) the genetic correlation r_G between similar traits measured in the three levels and (2) the genetic correlation r_g among various environments within a level of the programme. A further definition of the subscripts is given in Figure 1. Most studies on G x E reported in the literature concern the genetic correlations between similar traits in central test and on-farm test environment (e.g. Bampton et al., 1977; Standal, 1977; Schulte-Coerne and Simon, 1978; Roberts and Curran, 1981; Sönnichsen et al., 1984; Groeneveld et al., 1984 and Ollivier et al., 1984). Estimates of the genetic correlations between expressions of traits in central or on-farm test and in commercial fattening are only reported by Ketelaars (1979) and Claus et al. (1984). However, for a complete picture of the impact of G x E in pig breeding programmes, the genetic correlations between the levels (r_G) as well as the genetic correlations within the levels of the breeding programme (r_g) are needed.

In this series of papers the genetic correlations for the Dutch herdbook breeding programmes are reported successively. In the first place the genetic correlations within the nucleus (r_{gI}), multiplication (r_{gII}) and commercial fattening (r_{gIII}) level were reported (Merks, 1986, 1987c; Merks and Van Kemenade, 1987). The data of central and on-farm test were gathered within the framework of the herdbook breeding programme. A progeny test of AI-boars was started to obtain the commercial fattening data. To complete the analysis of the G x E-problem in pig breeding programmes, the genetic correlations between similar traits measured in central test, on-farm test and commercial fattening (r_{G1}, r_{G2} and r_{G3}) are reported in this paper.

MATERIAL AND METHODS

The central test and on-farm test data used in previous analyses (Merks, 1986, 1987b) were extended with the data of such a period that the own performance records of the sires used in the progeny test under commercial fattening conditions (Merks and Van Kemenade, 1987) were included. The central test data were gathered between April 1979 and August 1981 on three stations and between April 1979 and July 1983 on the fourth and largest Dutch test station. Dutch Landrace (NL) and Dutch Yorkshire (GY) breeds were both represented on all stations. The test procedure on these stations for boars and gilts was described by Merks (1986). All pigs tested were included in the breeding value estimation procedure.

The set of NL and GY on-farm test data used by Merks (1987b) was extended with data gathered in 1984. So the dataset consisted of gilts tested between May 1980 and December 1984, whereas the boars were tested between May 1982 and December 1984. A description of the on-farm test is given by Merks (1987b). For each breed-sex combination only herds with data on at least 20 tested animals per year have been selected to obtain a set of representative multiplication herds. Next to that sires were required to have progeny in at least 5 herds to avoid confounding of sire with herd effects.

To estimate breeding values of sires based on progeny performance in commercial fattening herds a progeny test of GY-AI-boars was started. The design of the progeny test is described by Merks and Van Kemenade (1987). These data have been used in this paper. In Table I all data used are summarized.

Table I. Summary of data used in the analyses by breed of the sires and sex of the progeny.

	CENTRAL TEST	ON-FARM TEST male	ON-FARM TEST female	COMMERCIAL FATTENING
Dutch Landrace (NL)				
sires	324		244	
litters	3345		23969	
stations/herds	4		270	
pigs tested ♂	6586		-	
pigs tested ♀	2864		58650	
Dutch Yorkshire (GY)				
sires	391	242	207	107
litters	4491	11944	7920	2609
stations/herds	4	200	152	35
pigs tested ♂	8798	37526	-	} 8148
pigs tested ♀	4165	-	17855	

Genetic correlations between performances in central test, on-farm test and commercial fattening were derived from the correlations between breeding values of sires in each level. Best linear unbiased predictions of breeding values were obtained for each data set by the computing algorithm of Schaeffer and Kennedy (1986) according to model 1. For each level of the breeding programme a different definition of the environmental effects (HYS) was used. For central test the fattening results were classified according to station-batch and carcass characteristics according to station-month classes (Merks, 1986). For on-farm test results HYS was defined as herd-year-season effects with two seasons; from March through September and from October through February (Merks, 1987b). For commercial fattening the results were classified according to herd-year-season-dam's breedtype classes. For seasonal effects month of arrival at the fattening herd was chosen (Merks and Van Kemenade, 1987).

$$\underline{y}_{ijk} = HYS_i + \underline{L}_{j:i} + \underline{a}_{k:ij} + \underline{e}_{ijk} \qquad \text{(model 1)}$$

where,

- $\underline{y}_{ijk}$ = the record of the k-th animal
- HYS_i = the (fixed) effect of the i-th environmental effect (HYS)
- $\underline{L}_{j:i}$ = the (random) effect of the j-th litter within the i-th HYS
- $\underline{a}_{k:ij}$ = the (random) additive genetic effect of the k-th pig in the ij-th litter
- $\underline{e}_{ijk}$ = the residual error.

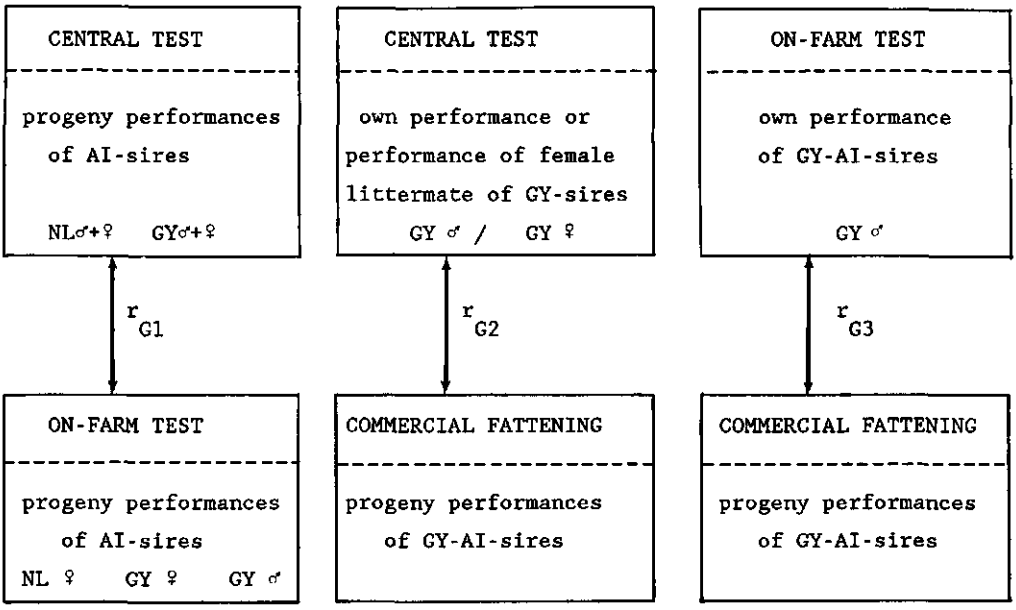

Figure 2. Schematic description of the genetic correlations estimated between the three levels in the herdbook breeding programme.

Variances of litters, pigs and residuals (σ^2_L, σ^2_a and σ^2_e) have been assumed constant over all i, j and k. Covariances among $\underline{a}_{k:ij}$ were included by using the numerator relationships among pigs. All other covariances among random elements of the model were assumed zero. However, for the estimation of breeding values of sires based on own performance in central or on-farm test only relationships between littermates were taken into account. The computing strategy,

described by Schaeffer and Kennedy (1986), used an iterative procedure to predict BLUP of breeding values which was stopped when the average absolute change in animal solutions was less than 0.1 % of one standard deviation of animal solutions.

A schematic description of the correlations estimated is given in Figure 2. The genetic correlations between central and on-farm test for similar traits have been derived from the correlations between sires' progeny performance in both environments. The correlations were obtained within each breed separately for the male and female on-farm tested progeny. The breeding values of sires based on progeny performance in commercial fattening were related to the breeding values of these sires (or female littermates of central-tested sires) based on own performance results in central or on-farm test. The numbers of sires involved in the comparisons are tabulated in Table II along with the average numbers of progeny. The genetic correlations were derived from the correlations between breeding values using approximation procedures outlined by Blanchard et al. (1983). The correlation between the breeding values of s sires in environment 1 with the breeding values of the same sires in environment 2 ($r_{\hat{A}1\hat{A}2}$) is related to the genetic correlation (r_g) as follows:

$$r_g = \sqrt{\frac{\sum_i b_{i1} \sum_i b_{i2}}{\sum_i b_{i1} b_{i2}}} * r_{\hat{A}1\hat{A}2} \qquad (1)$$

where i = 1, ...s and b_{ij} is the regression of half the breeding value of sire i on the progeny average y_{ij} in environment; according to (2) or the regression of the breeding value of sire i on his own performance in environment j in which case $b_{ij} = h^2$.

$$b_{ij} = \frac{0.25h^2 mn}{1+0.25h^2(n(m+1)-2)+c^2(n-1)} \qquad (2)$$

where,

m = number of litters of sire i in environment j

n_2 = average number of pigs per litter of sire i in environment j

h^2_2 = heritability of the trait in environment j

c^2 = common environmental effect of littermates in environment j.

Table II. Summary of the data used for the estimation of the genetic correlations between the different levels of the breeding programme.

Sires with progeny results in central (CT) and on-farm test (FT) by breed of the sires and sex of the progeny.

breed	sex CT	sex FT	number of sires	progeny in central test litters/sire	progeny in central test pigs/litter	progeny in on-farm test litters/sire	progeny in on-farm test pigs/litter
NL	♂	♀	147	11.8	2.0	109.2	2.5
NL	♀	♀	131	10.8	1.0	114.6	2.5
GY	♂	♂	131	13.9	2.0	42.0	2.4
GY	♂	♀	127	13.5	2.0	60.0	3.3
GY	♀	♂	121	13.9	1.0	42.4	2.4
GY	♀	♀	117	13.6	1.0	62.3	3.3

Sires of the GY breed with progeny results in commercial fattening environment and own performance in central (CT) or on-farm (FT) test

own/sib performance	number of sires	progeny in fattening environment litters/sire	progeny in fattening environment pigs/litter
FT	38	22.4	3.5
CT	54	22.4	3.4

Variance components, heritabilities and common environmental components used were from previous analyses (Merks, 1986, 1987a, 1987b; Merks and Van Kemenade, 1987).

The genetic correlations across levels of the breeding programme were estimated only for traits with a similar definition. In Table III a short description of the similar growth and the similar carcass quality traits is given. Traits measured in the different levels of the breeding programme that are assumed to be identical traits are written on the same row. Growth rate measured in central test as daily gain on test (DGT), weight for age (W/A) and daily

Table III. Short description of similar growth and similar carcass quality traits in the different levels of the breeding programmes (identical traits are on the same row).

CENTRAL TEST	ON-FARM TEST	COMMERCIAL FATTENING
- Daily gain on test (DGT: 25-100 kg)		
- Weight for age (W/A: birth-100 kg)	- Weight corrected for age (SC W: birth-100 kg)	- Daily gain during life (DGL: birth-108 kg)
- Daily gain on station (DGS: arrival-100 kg)		- Daily gain during fattening (DGF: arrival-108 kg)
- Ultrasonic backfat thickness (UB: 100 kg)	- Backfat thickness corrected for age (SC UB: 100 kg)	
- Carcass backfat thickness (CB: 75 kg)*.		
- Score for carcass backfat thickness (BC: 75 kg)*.		- Score for carcass backfat thickness (BC: 83 kg)*.
- Ham + loin percentage (HL: 75 kg)*.		
- Score for type (T: 75 kg)*.		- Score for type (T: 83 kg)*.

*) carcass weight.

gain on station (DGS), have each been related to weight corrected for age (SC W) in on-farm test and to daily gain during fattening (DGF) and daily gain during life (DGL) in commercial fattening. For carcass quality ultrasonic backfat thickness (UB) measured on central tested boars has been related to backfat thickness corrected for weight (SC UB) in on-farm test and to the scores for carcass backfat thickness (BC) and type (T) in commercial fattening. Besides that, carcass backfat thickness (CB), ham + loin percentage (HL) and the scores for carcass backfat thickness (BC) and type (T) measured on female progeny or littermates of the central tested sires have been related to SC UB in on-farm test and BC and T in commercial fattening.

RESULTS

The genetic correlations between similar traits measured in central and on-farm test (r_{G1}) are tabulated in Table IV for daily gain and ultrasonic backfat thickness. Results of central-tested male progeny groups were related to the results of male and female on-farm tested progeny groups of the same sires. The genetic correlations for daily gain ranged from 0.27 to 0.65. The differences between the correlations for the different definitions of daily gain in central test were small. The genetic correlations between UB and SC UB were all close to each other; r_{G1} = 0.50 - 0.70. For GY the male-male comparison resulted in higher genetic correlations than the male-female comparison.

Table IV. Genetic correlations between central and on-farm test (r_{G1}) based upon male progeny performance in central test (CT) and male or female progeny performance in on-farm test (FT) (correlations between breeding values in brackets).

CT	FT	DGT SC W	DGS SC W	W/A SC W	UB SC UB
NL ♂	NL ♀	0.57(0.35)	0.50(0.25)	0.65(0.30)	0.66(0.45)
GY ♂	GY ♀	0.46(0.25)	0.27(0.14)	0.29(0.17)	0.50(0.33)
GY ♂	GY ♂	0.42(0.24)	0.35(0.20)	0.41(0.25)	0.70(0.48)

The genetic correlations between different carcass characteristics measured on central tested gilts and ultrasonic backfat thickness measured on on-farm tested gilts and boars (r_{G1}) are tabulated in Table V. All correlations were favourable. Generally, the female-female comparison resulted in higher genetic correlations than the female-male comparison.

Table V. Genetic correlations between central and on-farm test (r_{G1}) based upon female progeny performance in central test (CT) and male or female progeny performance in on-farm test (FT) (correlations between breeding values in brackets).

CT	FT	CB		HL		BC		T	
		SC	UB	SC	UB	SC	UB	SC	UB
NL ♀	NL ♀	0.75(0.53)		-0.31(-0.20)		0.50(0.30)		-0.30(-0.17)	
GY ♀	GY ♀	0.29(0.21)		-0.43(-0.32)		0.60(0.31)		-0.55(-0.31)	
GY ♀	GY ♂	0.30(0.22)		-0.39(-0.30)		0.40(0.22)		-0.36(-0.21)	

In Table VI the genetic correlations between the own performance results of GY sires and sires' progeny performance in commercial fattening are given. The genetic correlations for daily gain between central test and commercial fattening (r_{G2}) do not significantly deviate from zero. However, moderately high genetic correlations are calculated between the ultrasonic backfat thickness (UB) of the sires and carcass grading of their progeny (BC and T). Moderately high correlations are also found between carcass characteristics measured on central tested female littermates of the sires and the carcass grading of their commercially fattened progeny. For the latter comparison only 30 sires were used because the other 13 sires had no data on central tested female littermates.

The genetic correlations between the own performance of sires in on-farm test and sires' progeny performance in commercial fattening (r_{G2}) were around one for daily gain (Table VI). However, no clear relationship was found between the ultrasonic backfat thickness of the sires and the carcass grading of their progeny. Nevertheless, the genetic correlations between the index of the on-farm tested sires and their progeny performance were all moderate to high.

Table VI. Genetic correlations between performances of GY sires in central (r_{G2}) or on-farm test (r_{G3}) and their progeny performance in commercial fattening environment (correlations between breeding values in brackets).

	Commercial fattening			
Central test	DGF	DGL	BC	T
DGT	-0.21(-0.05)	-0.48(-0.13)		
DGS	0.17(0.04)	-0.07(-0.02)		
W/A	0.04(0.01)	-0.21(-0.07)		
UB			0.46(0.18)	-0.44(-0.18)
CB			0.03(0.01)	-0.03(-0.02)
HL			-0.21(-0.10)	0.29(0.14)
BC			0.64(0.18)	-0.67(-0.19)
T			-0.60(-0.17)	0.57(0.17)
On farm test				
SC W	1.13(0.31)	0.94(0.29)		
SC UB			-0.09(-0.04)	0.15(0.06)
INDEX	0.90(0.25)	0.75(0.24)	-0.54(-0.18)	0.33(0.11)

DISCUSSION

The concept of the genetic correlation as a parameter that expresses G x E is based on the idea that the expression of identical traits in different environments may in fact not be controlled by the same sets of genes. However, in most studies on G x E the traits measured in the different levels of the breeding programme were not identical (e.g. Standal, 1977; Groeneveld et al., 1984). To quantify the effect of different definitions of traits, similar traits have been included in the comparison next to identical traits. In on-farm test data it has been shown that SC W and SC UB are identical to W/A and UB respectively (Merks, 1987b). The correlations between different traits measuring daily gain in central test and SC W in on-farm test showed some differences, but they were small. For carcass characteristics differences in

definition of the traits measured were more important; the genetic correlations between SC UB and UB were in general much higher than those between SC UB and CB or BC. These differences are in agreement with the genetic correlations between the different definitions of daily gain and of carcass quality as estimated for central tested pigs (Merks, 1986). So, the magnitude by which the genetic correlations between levels of the breeding programme are lowered if similar but not identical traits are correlated, may be predicted from the correlations between these traits if all are measured on the same animals. Especially for carcass traits this troublesome factor should be taken into account.

The existence of sex x environment interaction is another factor that might contribute to the G x E problem. Indications for sex x environment interaction are reported by Roberts and Curran (1981) and Sellier et al. (1985) and are also present in this study. Within the GY breed, UB and BC have a higher correlation with SC UB for respectively the male-male and female-female comparison than for the comparisons with progeny of different sex. For daily gain there are no consistent indications for sex interaction between on-farm test and central test environment, but in general the comparison of station-male and farm-female progeny resulted in somewhat lower genetic correlations than the comparison of male progeny in both environments. These indications for sex x environment interactions may be due to the sire x sex interactions reported for SC UB (r_g = 0.85) and SC W (r_g = 0.90) in on-farm test results.

The genetic correlations for identical traits between central and on-farm test (r_{G1}) are comparable or somewhat lower than the genetic correlations for these traits between sires' progeny in different multiplication herds (Merks, 1987c). From this it may be concluded that the test stations have an environment similar to the environment in a single multiplication herd with on-farm testing. Since the on-farm test breeding values of sires are more or less equal to the 'average' performance of their progeny in different environments, the genetic correlation between sires' progeny groups in different herds is an upper limit for the correlation between on-farm test results and results in other environments like central test. This is in agreement with the more general statement about the upper limit for r_G of Brascamp et al. (1985). Despite the moderate correlations between central and on-farm test results, central test stations still may have advantages. Advantages might be the prevention of preferential treatment, higher genetic variance and the possibilities to meas-

ure traits that are too expensive or even impossible to measure in on-farm test.

The genetic correlations obtained in this study between central test and on-farm test were somewhat higher than most correlations reported in literature (Table VII), but similar to the estimates of Standal (1977), Sönnichsen et al. (1984) and Sellier et al. (1985). The lower genetic correlations reported in some studies may be due to their data structure; sires and dams nested within herds. Especially in case sire x herd interactions are present in on-farm test results, this nested structure will contribute to an underestimation of the genetic correlations between different levels of the breeding programme.

Table VII. Summary of genetic correlations in literature between progeny performance in central test (CT) and on-farm test (FT) for daily gain and backfat thickness.

Source		sex of progeny CT	FT	daily gain [1]	backfat thickness [2]
Standal (1977)		♀	♂	0.45	0.65
Bampton et al. (1977)		♂	♀	0.23	0.34 [3]
Schulte Coerne and Simon (1978)		♀	♂	0.06	0.08
Roberts and Curran (1981)		♂	♂	0.02	0.46 [3]
		♂	♀	-0.01	0.35 [3]
Groeneveld et al. (1984)		♀	♂	0.08	0.20
Sönnichsen et al. (1984)		♀	♂	0.20	0.72
Sellier et al. (1985)		♂	♂	0.45	0.32
		♂	♀	0.30	0.48
This study	GY	♀	♂	0.42	0.30
	GY	♀	♀	0.46	0.29
	NL	♀	♀	0.57	0.75

1) daily gain on test in CT and weight for age in FT
2) carcass backfat thickness in CT and ultrasonic backfat thickness in FT
3) 'C' fat depth in CT as well as FT

The comparison of progeny results in commercial fattening and the performances of the sires in central test (r_{G2}) showed no clear relationship for daily gain characteristics. This might be the result of the low genetic correlations for DGF and DGL between sires' progeny performance in different fattening herds (Merks and Van Kemenade, 1987). The genetic correlations between carcass classification in commercial fattening and carcass characteristics in central test were except for CB and HL about equal to correlations between these traits measured on the same animals (Merks, 1986). This is in agreement with the absence of sire x herd interaction in commercial fattening results for BC and T (Merks and Van Kemenade, 1987). Ketelaars (1979) reported lower genetic correlations between central test and commercial fattening results for backfat thickness (r_{G3} = 0.03 - 0.05), but higher correlations for daily gain (r_{G3} = 0.16 - 0.59).

The genetic correlations between on-farm test and commercial fattening for daily gain and carcass quality are not consistent with each other; for daily gain r_{G3} = 0.94 - 1.13, for carcass quality r_{G3} = -0.09 - 0.15. The very high correlations might be due to chance. The sire x herd interaction in on-farm test results (Merks, 1987c) may be responsible for the inconsistency since the breeding values for the sires in on-farm test are based on own-performance. It is difficult to derive conclusions from the correlations between on-farm test and commercial fattening, but certainly they are favourable for daily gain. A more accurate and reliable relationship may be obtained by a progeny test of sires in each of the levels of the breeding programme as suggested by Standal (1984).

The genetic correlations reported between commercial fattening on the one hand and central test or on-farm test on the other, may be influenced by the comparison of pure-bred pigs in central or on-farm test and crossbred pigs in commercial fattening. Standal (1968) and McLaren (1985) reported correlations smaller than one between pure-bred and crossbred progeny fattened in the same herd.

The breeding values estimated on basis of on-farm test and commercial fattening results were not corrected for the sire x herd interactions. This may have resulted in an underestimation of the genetic correlations, but probably only to a small extent as Bertrand et al. (1987) reported a small effect of this correction in beef cattle field data. Next to that, the genetic correlations obtained were approximated and may be biased due to heterogeneity of

variances in on-farm test and commercial fattening data. Further development of mixed model procedures and computing strategies will help to overcome these problems.

From the results in this paper, the existence of moderate genetic relationships between the different levels of the breeding programme may be concluded. The main factor hold responsible for these moderate relationships is the sire x herd interaction in on-farm test and commercial fattening. Differences between the levels in for instance feeding regimen or housing system may have contributed to the moderate relationships, but the environmental differences generated by these factors are small compared to the differences in environmental conditions between herds. The moderate genetic correlations, especially those between central or on-farm test on the one hand and commercial fattening on the other, require adaptation of the breeding programme. Selection on basis of a combination of performances in central test and performances of sibs in on-farm test or commercial fattening may be an efficient alternative. According to the calculations of Brascamp et al. (1985), the genetic correlations estimated in this study may even be in favour of two stage selection with progeny testing in the second stage. In the last paper of this series, the consequences of the reported genetic relationships for the design of the breeding programme will be worked out further.

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CHAPTER 7

CONSEQUENCES FOR DESIGN AND EFFICIENCY OF PIG BREEDING PROGRAMMES

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ABSTRACT

In a pig breeding programme the effect of genotype x environment interaction may be expressed as the genetic correlation r_G between identical traits measured in the different levels and as r_g, the genetic correlation within a level of the breeding programme. In this paper the consequences of moderate values for these correlations for the design and efficiency of pig breeding programmes are investigated.

In general, the accuracy of selection across levels of the breeding programme on basis of sib or progeny information is directly proportional to $(r_G/[r_{gP} * r_{gH}]^{\frac{1}{2}})$. Here r_{gP} and r_{gH} are the genetic correlations within respectively the level where the index information is collected and the level where the breeding goal is defined. The best use is made of a limited number of test places by distributing the representatives of the genotype over as many herds or environmental classes as possible. The size of r_G in comparison with r_g is discussed further as this has a large impact on the efficiency of pig breeding programmes. For a fixed r_G, the highest genetic progress may be achieved if $r_{gP} = r_G$.

Furthermore, some testing strategies are compared for their expected genetic progress under the circumstances of values for r_g and r_G as reported in the previous papers of this series. From this it was concluded that in general testing of boars and simultaneously their paternal half sibs in on-farm test or commercial fattening is depending on the parameters almost 3 times more efficient than central testing only. Also two-stage selection with progeny testing in commercial fattening appeared an efficient alternative.

INTRODUCTION

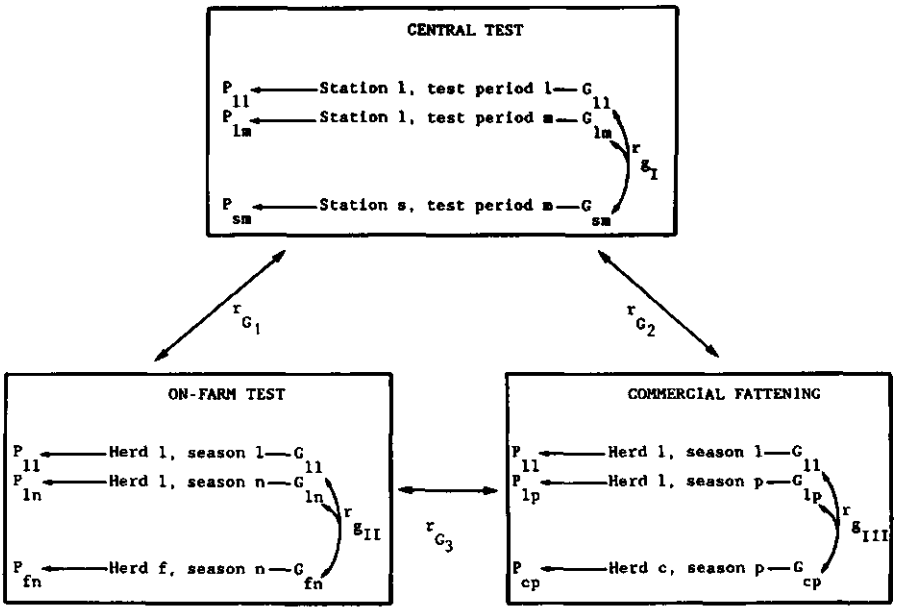
A pig breeding programme generally consists of different levels indicated as nucleus, multiplication and commercial fattening level. Selection takes place at all levels but selection in the nucleus determines eventually the rate of annual genetic change. This genetic change is of economic importance at all levels but especially at commercial fattening because of its relatively large number of animals. Therefore, the breeding goal has to be defined at the level of commercial fattening.

Interaction of genotype and level of the breeding programme may decrease the efficiency of pyramidal breeding programmes to a large extent. In different studies low to moderate genetic correlations between similar traits at different levels of the breeding programme have been reported (e.g. Standal, 1977; Ketelaars, 1979; Claus et al., 1984; Groeneveld et al., 1984; Ollivier et al., 1984; Merks, 1987d). These low to moderate correlations between levels seem mainly due to the moderate genetic correlations between sires' progeny in different herds for on-farm test (Merks, 1987c) as well as for commercial fattening results (Merks and Van Kemenade, 1987). If there are several major consistent categories of environmental factors between which the relative suitability of genotypes does change importantly, development of special purpose breeding stock might be relevant (Webb and Curran, 1986). However, the environmental differences between herds, multiplication as well as commercial fattening herds, are numerous and sometimes undefinable. Therefore, selection of genetic stock for suitability under the environmental conditions of commercial fattening herds seems most appropriate. This may require reappraisal of the present breeding programmes.

The purpose of this paper is to investigate the consequences of the moderate genetic correlations between and within the different levels of a pig breeding programme for its design and efficiency. Firstly some general rules for the efficiency of selection under these circumstances are discussed. Thereafter the efficiency of some breeding programmes is determined and discussed with regard to the optimal design of breeding programmes.

GENERAL CONSEQUENCES FOR THE EFFICIENCY OF SELECTION

The effect of genotype x environment interaction (G x E) on the efficiency of breeding programmes is inversely proportional to the genetic correlation among genotypes in the different environments for identical traits (Falconer, 1952). Especially in case of low to moderate genetic correlations, G x E requires reappraisal of breeding programmes (Brascamp et al., 1985). Pig breeding programmes are in general complex due to different levels in a pyramidal structure. Therefore, some general rules for the efficiency of selection within and across levels are derived.



A pig breeding programme with three levels is assumed (Figure 1); nucleus herds with central testing (CT), multiplication herds with on-farm testing (FT) and commercial herds with fattening pigs (CF). The genotype x environment interaction between the different levels is represented by r_G, while r_g represents the genotype x environment interactions within a level of the pyramid. It has been assumed that the genetic correlation between two levels (r_G) is equal to or smaller than the genetic correlation (r_g) within each of these two levels. The breeding goal is defined at the level of commercial fattening as the suitability of the genotype on an average fattening herd.

Selection within a level of the breeding programme

Firstly, the efficiency of selection is worked out for the situation where selection is based on information obtained at the level at which the breeding goal is defined. This situation concerns the level of commercial fattening in the breeding programme assumed. Dickerson (1962) showed that the genetic change per generation (ΔG_N) in average performance measured in N herds from selecting within these herds simultaneously, relative to that from selection

based on measurements in a single herd (ΔG_1), is dependent upon the number of herds (N) and the genetic correlation between the genotypes in the different herds (r_g), as follows:

$$\frac{\Delta G_N}{\Delta G_1} = \sqrt{\frac{N}{1+(N-1)r_g}} \qquad (1)$$

However, for a fair comparison the total numbers (Nmn) of individuals tested per genetic group should be kept constant. Therefore, it has been assumed that each sire has m litters of size n on N herds in case of selecting on these herds simultaneously, and Nmn individuals per sire in case of selection in a single herd. It is worked out in the Appendix that with equal selection intensities formula (1) in that situation becomes:

$$\frac{\Delta G_N}{\Delta G_1} = \left[\frac{(1+(n-1)(0.5h^2+c^2) + n(mN-1)0.25h^2}{(1+(n-1)(0.5h^2+c^2) + n(m-1)0.25h^2 + nm(N-1)0.25h^2 r_g}\right]^{\frac{1}{2}} \qquad (2)$$

Here, c^2 stands for the non additive genetic relationship between littermates within herds and h^2 for the heritability of the trait. From this formula it may be concluded, that the advantage of increasing N is simply to minimise error from r_g in measuring the suitability of each genotype over an increased number of herds. Consequently, the best use is made of a certain number of test places in different herds by distributing the representatives of the genotype over as many herds as possible.

Own performance testing is not of interest in commercial fattening because of the low heritabilities. The accuracy of selection (r_{IH}) on basis of sib or progeny results is, besides number of sibs/progeny and heritability, a function of the number of herds (N) and r_g. For a equal to the additive genetic relationship between index and breeding goal animals, the accuracy of selection within commercial fattening becomes:

$$r_{IH} = \left[\frac{a^2 r_g h^2 Nmn}{(1+(n-1)(0.5h^2+c^2) + n(m-1)0.25h^2 + nm(N-1)0.25h^2 r_g)}\right]^{\frac{1}{2}} \qquad (3)$$

Here, h^2 and c^2 are defined at the level of commercial fattening. Note that if the number of herds becomes very large ($N \to \infty$), the maximum accuracies of progeny and half sib information are equal to the well known values of 1 and 0.5 respectively.

In Figure 2 the effect of the total number of progeny (m-n-1) per sire on the accuracy of progeny testing (r_{IH}) is shown for different combinations of r_g (respectively 0.8, 0.5 and 0.2) and h^2 (respectively 0.3 and 0.1). An important increase in accuracy of selection is made with an increase in numbers of progeny up to 100, or even up to 200 for traits with a low r_g and or h^2. However, in Figure 2 maximal profit is made from an extra descendant because it is tested in again another herd. For pigs this is a theoretical situation. In practical circumstances there will be more than one pig per litter and more litters per herd. The effect on r_{IH} of more litters per sire and herd instead of distributing these litters over different herds, is limited (less than 10 %) if only 2 or 3 litters (with each 1 pig/litter) are tested per herd.

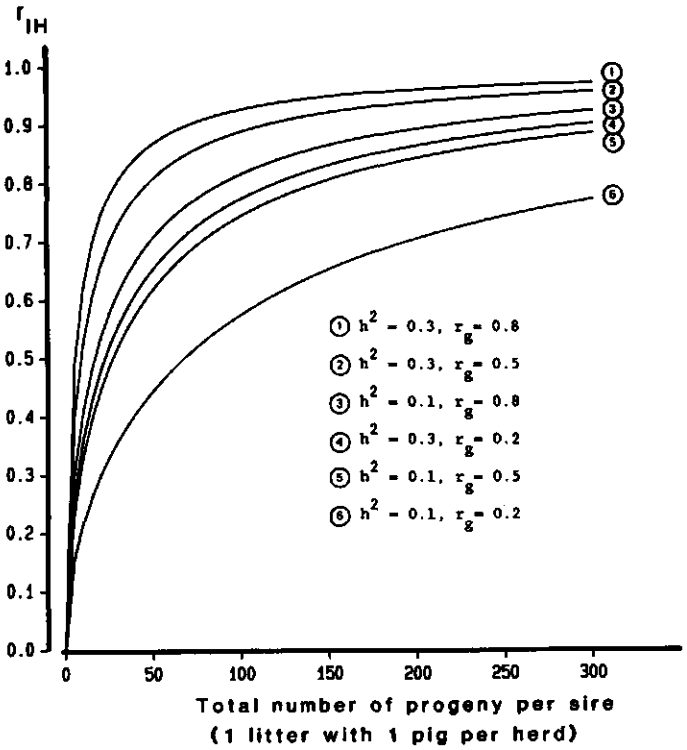


Figure 2. The accuracy of selection (r_{IH}) within a level of the breeding programme in dependency of the number of progeny (N) and for different combinations of r_g and h^2.

The effect of r_g on the genetic progress (ΔG) comes partly from the effect on r_{IH}, but also from the effect on σ_H, the standard deviation of the breeding goal trait. In case $r_g < 1$, σ_H is directly related to r_g. Nevertheless, the same ranking of the different combinations of r_g and h^2_g would appear in Figure 2, if ΔG was plotted instead of r_{IH}.

Selection across levels of the breeding programme

Selection across levels of the breeding programme is defined here as selection using information from one level while the breeding goal is defined at another level. In the breeding programme described this concerns selection on basis of on-farm test or central test results. Two situations are distinguished; (1) selection on own performance only and (2) selection on sib or progeny information. In the first situation the own performance of a potential breeding animal is measured in a certain multiplication herd or test period in central test. It is shown in the Appendix that the accuracy of selection on own performance ($r_{IH}(OP)$) is a function of the genetic correlation within the breeding goal level (r_{gH}) and the genetic correlation across levels of the breeding programme (r_G):

$$r_{IH}(OP) = \frac{r_G h}{\sqrt{r_{gH}}} \qquad (4)$$

where h equals the square root of heritability of the index trait.

In the second situation, progeny or sibs results are collected in central or on-farm test. The accuracy of selection across levels is a function of the genetic correlations within index (r_{gP}) and breeding goal level (r_{gH}) and the genetic correlation between these two levels (r_G):

$$r_{IH} = \left[\frac{a^2 r_G^2 h^2 \, Nmn}{(1+(n-1)(0.5h^2+c^2) + n(m-1)0.25h^2 + nm(N-1)0.25h^2 r_{gP}) * r_{gH}} \right]^{\frac{1}{2}} \qquad (5)$$

Here, h^2 and c^2 are defined at the level where the index information is obtained. It is shown in the Appendix that the maximum accuracy of selection

r_{IH} (max) across levels of the breeding programme on basis of progeny or half sib information is equal to:

$$r_{IH}\ (max) = \left[\frac{4a^2 r_G}{r_{gP} * r_{gH}} \right]^{\frac{1}{2}} \qquad (6)$$

Note that if genotype x environment interaction is absent within levels ($r_{gP} = r_{gH} = 1$), the maximum accuracy of progeny information is equal to r_G.

In Figure 3 the effect of the total number of progeny (m=n=1) per sire on the accuracy of progeny testing is shown for different combinations of r_{gP}, r_G and r_{gH} (each with values of 0.7 and 0.4, further $r_G \leq r_{gP}$ and $r_G \leq r_{gH}$). For

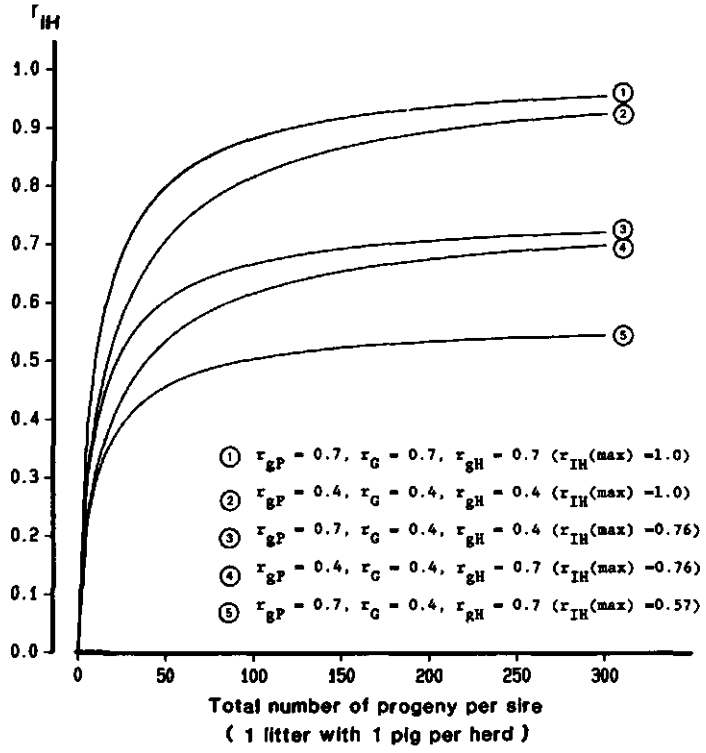


Figure 3. The accurary of selection (r_{IH}) across levels of the breeding programme in depency of the number of progeny (N) and for different r_{gP}, r_G and r_{gH} (h^2 = 0.20).

the heritability of the index trait 0.2 was chosen. The maximum values for r_{IH} for each combination of r_{gP}, r_G and r_{gH} are given in the legend. It should be noted that also in Figure 3 profit from an extra descendant is maximal because it is tested in again another herd. The accuracy of selection appeared mainly a function of r_G. An increase in r_{gP} or r_{gH} has, for a given r_G, a negative effect on r_{IH}. The larger the difference between r_g and r_G, the larger the genetic difference between the traits measured at the two levels. Especially the difference between r_{gH} and r_G is important. Consequently, the information of the index traits becomes less relevant. For a fixed r_G, the highest r_{IH} is reached if $r_{gH} = r_G = r_{gP}$.

However, the genetic progress (ΔG) is not only a function of r_{IH}. In case $r_{gH} < 1$, σ_H is directly related to r_{gH}. This has an important effect on the ranking of the different combinations of r_{gP}, r_G and r_{gH} when ΔG is plotted instead of r_{IH}. The ranking for ΔG will be according to the values for r_{IH} (max) * r_{IH}. So the relative genetic progress for the 5 combinations of r_{gP}, r_G and r_{gH} will be 0.84, 0.63, 0.48, 0.63 and 0.48 respectively. From this follows that differences in r_{IH} may be of minor importance for ΔG. For a given r_G, the highest ΔG may be reached if $r_{gP} = r_G$.

COMPARISON OF THE EFFICIENCY OF THREE BREEDING PROGRAMMES

To obtain a better understanding of the consequences of G x E for the efficiency of pig breeding programmes, three alternatives for a single trait programme have been compared for two sets of genetic parameters. All alternatives have a pyramidal breeding structure with three levels; nucleus, multiplication and commercial fattening. The breeding goal is defined on the level of commercial fattening. Only the selection of boars in the nucleus is considered in the comparison, sows for replacement are chosen at random. The selection on the levels of multiplication and commercial fattening has been assumed to be equal for the 3 programmes and is therefore not considered. The three programmes were chosen on basis of the present situation in most breeding programmes and next to that alternatives that use, enabled by usage of AI, progeny or sib information from on-farm test or commercial fattening. In Figure 4 the three programmes are illustrated. The breeding structure of programme 2 and 3 is comparable to system 1 and 2 of Brascamp et al. (1985).

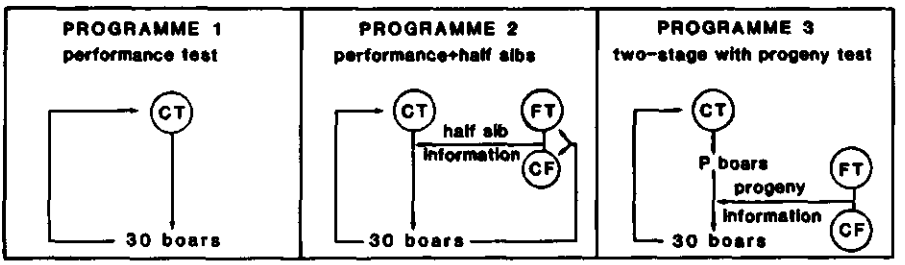


Figure 4. Schematic description of the 3 breeding programmes that are compared (with CT = central test, FT = on-farm test, CF = commercial fattening and P boars are selected in the first stage of programma 3).

To make a fair comparison of the three programmes, the total costs for each of the 3 programmes was kept equal. It has been assumed that the costs of a testing place in central test, on-farm test and commercial fattening were 75, 25 and 1 respectively and that the total costs were equal to 1500 x 75. To obtain the maximal genetic progress with the information from on-farm test or commercial fattening, the progeny or half sibs of each sire have been spread over as many herds as their number. In each programme 30 boars are selected to produce the next generation of young boars.

Description of the programmes

A general description of the three programmes is given below:

Programme 1 (P1): only central testing of boars is used for selection, 1500 individual places are available each year. From the boars tested, the 30 best boars are selected on basis of own performance and the central test results of 49 paternal half sibs (49 = (1500/30 - 1). Batchwise testing of the half sib groups is necessary for this number of half sibs. For both boars and sows a generation interval of 1 year has been assumed, so in total a generation interval of 2 years.

Programme 2 (P2): next to performances in central test, the results of paternal half sibs in on-farm test (P2A) or commercial fattening (P2B) are included in the selection. These results are obtained by having breeding boars producing progeny for both central test and on-farm test/commercial

fattening simultaneously. The number of central test and on-farm test/commercial fattening places was optimized with respect to the genetic progress per generation; central test capacity was decreased with steps of 100 places to increase on-farm test or commercial fattening capacity with 300 or 7500 places respectively. The 30 best boars are selected on basis of an index combining own performance in central test and the results of their paternal half sibs in on-farm test (P2A) or commercial fattening (P2B). For both boars and sows a generation interval of 1 year has been assumed, so in total 2 years.

Programme 3 (P3): two-stage selection is applied. The selection in the first stage is based upon own performance of the boars in central test. The selected boars are progeny tested in on-farm test (P3A) or commercial fattening (P3B). The 30 best boars are selected in the second stage on basis of an index combining own performance and progeny results and they produce the new generation of young boars for central test. The number of test places in central test and on-farm test or commercial fattening was optimized in combination with the number of progeny tested sires. The genetic progress per generation was the criterion to find the optimum; central test capacity was decreased with steps of 100 places to increase on-farm test or commercial fattening with 300 or 7500 respectively places and each step the number of progeny tested sires was decreased from half the number of central tested boars with steps of 50 down to 60 boars. A selection of more than 50 % was not worked out in first instance as it would in that case be better to chose a boar at random. For the boars a generation interval of 2 years has been assumed, for the sows 1 year, thus in total 3 years.

The genetic parameters used were derived from heritabilities and genetic correlations within and between levels of the breeding programme reported in the previous papers (Merks, 1987a, 1987b, 1987c and Merks and Van Kemenade, 1987) for daily gain (set 1) and ultrasonic backfat thickness (set 2). These two traits were chosen as representatives of traits with low (set 1) or moderate (set 2) genetic correlations between and within levels of the breeding programme. Adaptations in the parameters were made such that the genetic correlation between two levels (r_G) is equal to or smaller than the genetic correlation within each of the two levels (r_g). The parameters used are tabulated in Table I.

Table I. Two sets of genetic parameters * for identical traits measured in central test (CT), on-farm test (FT) or commercial fattening (CF) used to compare the efficiency of 3 pig breeding programmes.

	trait CT			trait FT			trait CF		
	h^2	c^2	σ^2_P	h^2	c^2	σ^2_P	h^2	c^2	σ^2_P
Set 1	0.20	0.15	50	0.20	0.20	60	0.10	0.20	70
Set 2	0.35	0.10	1.5	0.30	0.20	2.0	0.10	0.15	2.5

	r_{gI}	r_{gII}	r_{gIII}	r_{G1}	r_{G2}	r_{G3}
Set 1	1.0	0.5	0.4	0.45	0.2	0.4
Set 2	1.0	0.7	0.7	0.7	0.4	0.5

*) The genetic parameters are derived from the parameters reported in the previous papers of this series (set 1: daily gain, set 2: ultrasonic backfat thickness).

The genetic progress for each of the three programmes was calculated as $\Delta G = i * \sigma_I$, with i = selection intensity and σ_I = the standard deviation of the index. The calculation of ΔG is worked out in the Appendix. Because of truncation selection in the first stage of P3A and P3B, all variances and covariances in the second stage were reduced according to the formulae of Cochran (1951).

Results

The test capacity for both P2 and P3 was optimized first. The optimal number of test places and progeny tested sires (for P3) are tabulated in Table II (set 1) and III (set 2). For both breeding programmes less emphasis on central test occured for parameter set 1 than for parameter set 2. The genetic progress achieved with each of the programmes is also given in Table II and III. For both parameter sets, the breeding programme that makes use of half sib results in commercial fattening (P2B) is superior to the others. However, this superiority is small if compared with P3B and next to that a large part of the

Table II. Results of the optimized breeding programmes for parameter set 1.

	P1	P2A	P2B	P3A	P3B
Number of					
CT-places	1500	800	1200	300	600
FT-places	-	2100	-	3600	
CF-places	-	-	22500	-	67500
half sibs/animal	49	70	750	-	-
progeny tested sires	-	-	-	150	300
progeny/sire	-	-	-	24	225
Stage 1: own performance					
(+ half sibs) i	2.42	2.18	2.34	0.80	0.80
σ_I	2.37	5.22	6.73	1.99	1.99
$\Delta G_1 = i * \sigma_I$	5.73	11.39	15.77	1.59	1.59
Stage 2: own performance					
+ progeny test i				1.40	1.75
σ_I				7.51	11.60
$\Delta G_2 = i * \sigma_I$				10.51	20.30
$\Delta G_1 + \Delta G_2$	5.73	11.39	15.77	12.10	21.89
generation interval (years)	2.0	2.0	2.0	3.0	3.0
ΔG per year at fattening level	2.87	5.70	7.89	4.03	7.30
relative progress [1] /year	100	199	275	127	229
ΔG_{CT} per year at nucleus level [2]	15.31	11.99	12.08	7.03	7.15

1) The progress per year for P1 was assumed to be 100 %.
2) ΔG_{CT} is the genetic progress with the breeding goal defined at nucleus level instead of commercial fattening level.

Table III. Results of the optimized breeding programmes for parameter set 2.

	P1	P2A	P2B	P3A	P3B
Number of					
CT-places	1500	1100	1300	800	800
FT-places	-	1200	-	2100	-
CF-places	-	-	15000	-	52500
half sibs/animal	49	40	500	-	-
progeny tested sires	-	-	-	100	350
progeny/sire	-	-	-	21	150
Stage 1: own performance					
(+ half sibs) i	2.42	2.30	2.37	1.65	0.90
σ_I	0.21	0.24	0.34	0.19	0.19
$\Delta G_1 = i * \sigma_I$	0.52	0.56	0.82	0.31	0.17
Stage 2: own performance					
+ progeny test i				1.16	1.83
σ_I				0.31	0.54
$\Delta G_2 = i * \sigma_I$				0.36	1.00
$\Delta G_1 + \Delta G_2$	0.52	0.56	0.82	0.67	1.17
generation interval (years)	2.0	2.0	2.0	3.0	3.0
ΔG per year at fattening level	0.26	0.28	0.41	0.22	0.39
relative progress [1] /year	100	108	158	85	150
ΔG_{CT} per year at nucleus level [2]	0.72	0.65	0.65	0.46	0.39

1) The progress per year for P1 was assumed to be 100 %.
2) ΔG_{CT} is the genetic progress with the breeding goal defined at nucleus level instead of commercial fattening level.

accuracy of selection for P2B comes from the paternal half sibs. Exclusion of that half sib information in P2B, would result in 77 % (set 1) or 46 % (set 2) loss in progress. So in fact P2B is family selection and the intensity of selection should be adapted to that. In the extreme case one family out of 30 is selected; i = 2.24. The genetic progress (ΔG/year) for P2B and parameter set 1 and 2 becomes then respectively 7.69 and 0.39. The same should be done for P2A and parameter set 1. For parameter set 1 more progress may be achieved with P3B if the selection in the first stage (performance test) is dropped. In that case 750 random chosen young boars have to be progeny tested and the resulting progress/year would be 7.82, which is 7 % higher than reported for P3B in Table II.

The results for the same parameter sets and breeding structure but with the breeding goal defined at the nucleus level (ΔG_{CT}), are also given in Table II and III. The programme with only central testing (P1) is superior then for both parameter sets.

DISCUSSION

Selection under the environmental conditions where the production takes place (commercial fattening environment) is suggested by Falconer (1952) to overcome G x E. However, this is not a direct solution for pig breeding programmes because sire x herd interactions are present within commercial fattening (Merks and Van Kemenade, 1987). Selection of genotypes for general suitability under commercial conditions should be applied then. It may be brought up for discussion whether the breeding goal should incorporate the suitability of genotypes under all environmental conditions in commercial fattening. The environmental conditions of herds with below average results might be excluded, because it is not very likely that these environmental conditions are still relevant in the future. However, this selection of herds is only of interest if the size of r_G comes closer to the size of r_{gP}. Another possibility might be to focus the breeding goal on certain definable environmental factors and to standardise these factors in the whole breeding programme. This option will only be fruitful if there will be no major changes in these environmental factors for the next decades. Further research on the variation in r_g and the factors that determine the level of r_g may help to choose the appropriate breeding goal.

For the general consequences as well as for the comparison of the three programmes it has been assumed that the genetic correlations between two levels (r_G) is equal to or smaller than the genetic correlations within each of these two levels (r_g). This assumption seems justified as the correlation between the average performance of a genotype in different herds and the performance of the same genotype in another level of the breeding programme (r_G) must be equal to or smaller than the average correlation among the different herds (r_g). An indication for the relative size of r_G compared to r_g may be found in the consistency of the parameter sets. Meuwissen and Kanis (1987) indicated that the chance of an inconsistent parameter set is relatively high in situations with G x E. Foulley and Ollivier (1986) showed that for consistent parameter sets the eigenvalues of the C-matrix should be larger than 0 and those of the $C^{-1}G'P^{-1}G$-matrix should be between 0 and 1, where the C, P and G matrices are respectively the variance-covariance matrices of breeding goal and index traits and the covariance matrix between index and breeding goal traits . In a single trait situation the latter criterion means that $0 \leq r_{IH} \leq 1$. If this criterion is applied to the formulae for selection across levels of the breeding programme, it can be derived from formulae (6) that $0 \leq r_G \leq [r_{gP} * r_{gH}]^{\frac{1}{2}}$ for the situation of progeny information in the index. This result is somewhat different from the assumption made, but the assumption fits into this restriction.

The three breeding programmes were compared to show some of the consequences in a more practical situation. The best alternative should not be considered as the optimal programme under all circumstances. Especially assumptions about the selection intensities and the intensive use of AI might be difficult to fulfil in some breeding programmes. Further, the assumptions made about the relative costs of test places may not apply to practical programmes.

Generally, breeding programmes with performance testing in central test (with or without full sibs to be slaughtered) are accepted as the best (e.g. Minkema, 1973; Glodek, 1978; Niebel and Fewson, 1979), while programmes with progeny testing are considered to achieve less progress due to a prolonged generation interval. In this study a different ranking of these programmes was found. The programme with progeny testing in commercial fattening (P3B) achieved for both parameter sets more genetic progress than a programme with only performance testing in central test (P1). Somewhat more progress (5 - 20 %) was achieved with performance testing in central test and information

from paternal half sibs in commercial fattening (P2B). However, this alternative tends to family selection instead of individual selection and due to the small number of families (30) inbreeding may become a problem. For parameter set 1 somewhat more genetic progress may be achieved with P3B if the selection in the first stage would be dropped. In a practical situation this increase in genetic progress must be weighted against the possibility to measure traits like feed intake capacity and to have uniform rearing of potential AI boars. The differences in genetic progress between P2B and P3B and the number of test places needed for these programmes are in line with the model calculations of Brascamp et al. (1985): a large number of test places is needed in commercial fattening to make two-stage selection with progeny testing more efficient than performance testing with half sib information. The use of implantable electronic identification devices may facilitate the set up of such large scale progeny test.

In a practical situation most fattening pigs are crossbred pigs. Because of this, the programmes that make use of the results of fattening pigs, become a combination of individual and reciprocal recurrent selection. In other studies (e.g. Standal, 1968; McKay and Rahnefeld, 1984; McLaren et al., 1985) no clear advantage for reciprocal recurrent selection over mass selection is reported for daily gain and backfat thickness due to the prolonged generation interval. However, this disadvantage is not present if paternal half sibs are used and in the case of a progeny test the higher accuracy of selection counterbalances the prolonged generation interval. Reciprocal recurrent selection may even be part of the answer to G x E in pig breeding programmes because the low genetic correlations between test and commercial fattening environment may partly be due to the comparison of pure-bred and crossbred animals. In any case will the possibilities of including reciprocal recurrent selection in pig breeding programmes on a significant basis, open new dimensions for exploiting non-additive genes.

Generally it may be concluded that the moderate genetic correlations within and between levels of the breeding programme have a large impact on the genetic progress. Independent of the size of these genetic correlations, the most efficient design of a breeding programme is the one that uses on-farm test and/or commercial fattening results next to results of central testing. Testing of boars in central test and simultaneously their paternal half sibs in

on-farm test or commercial fattening is a promising possibility. Two stage selections with a progeny test under commercial fattening conditions is another possibility, but for an efficient design large numbers of fattening places and fattening herds are needed; about 100 - 150 litters distributed over 50 herds.

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APPENDIX

The effect of genotype x environment interaction within and across levels of the breeding programme on the efficiency of selection

Selection within a level of the breeding programme:

The selection is based on information from the level at which the breeding goal is defined. The aggregate genotype (H) is defined as the usefulness of each genotype on an average fattening herd according to:

$$H = \Sigma_i G_i / M \qquad (1)$$

here, i = 1, ...M and M is a very large number of herds ($M \to \infty$). The same results will be obtained with a breeding goal defined as the suitability of each genotype on a random herd. For index information each genotype is represented on N herds with m litters of size n. N is a random sample out of the M herds. The variance of this information (P_N) is equal to:

$$var(P_N) = [1+(n-1)(0.5h^2+c^2)+n(m-1)0.25h^2+nm(N-1)0.25h^2 r_g]\sigma_P^2/Nmn \qquad (2)$$

Here c^2 stands for the non-additive genetic relationship between full sibs within herds, h^2 for the heritability of the trait, r_g for the genetic correlation between sires' progeny in different and σ_P^2 for the variance of the trait. Further, for a equal to the additive genetic relationship between breeding goal and index individuals, $cov(P,H) = a r_g h^2 \sigma_P^2$. Finally, $var(H) = r_g h^2 \sigma_P^2$. The accuracy of selection ($r_{IH}(N)$) within a level of the breeding programme then becomes:

$$r_{IH}(N) = \left[\frac{a^2 r_g h^2 Nmn}{(1+(n-1)(0.5h^2+c^2)+n(m-1)0.25h^2+nm(N-1)0.25h^2 r_g)} \right]^{\frac{1}{2}} \qquad (3)$$

If the information of Nmn individuals per genotype is collected within one herd (N=1), the variance of this information (P_1) is equal to:

$$var(P_1) = [1+(n-1)(0.5h^2+c^2)+n(mN-1)0.25h^2]\sigma_P^2/Nmn \qquad (4)$$

The accuracy of selection $r_{IH}(1)$ on basis of this information is:

$$r_{IH}(1) = \left[\frac{a^2 r_g h^2 Nmn}{(1+(n-1)(0.5h^2+c^2)+n(mN-1)0.25h^2)} \right]^{\frac{1}{2}} \quad (5)$$

So, the genetic change per generation (ΔG_N) in average performance on N herds from selecting on these herds simultaneously, relative to that from selection in a single herd (ΔG_1) follows from (3) and (5) and is:

$$\frac{\Delta G_N}{\Delta G_1} = \left[\frac{(1+(n-1)(0.5h^2+c^2)+n(mN-1)0.25h^2}{(1+(n-1)(0.5h^2+ c^2)+n(m-1)0.25h^2+nm(N-1)0.25h^2 r_g} \right]^{\frac{1}{2}} \quad (6)$$

The genetic progress from selection on basis of progeny or sib information in different herds is equal to $\Delta G = i * \sigma_I$ or $\Delta G = i * r_{IH} * \sigma_H$, with i = selection intensity and for σ_I and σ_H the standard deviation of respectively index and breeding goal. Consequently, for selection within a level of the breeding programme ΔG equals:

$$\Delta G = i * \left[\frac{a^2 r_g^2 h^2 \sigma_P^2 Nmn}{(1+(n+1)(0.5h^2+c^2) + n(m-1)0.25h^2 + nm(N-1)0.5h^2 r_g)} \right]^{\frac{1}{2}} \quad (7)$$

Selection across levels of the breeding programme

The selection is based on information from a level different from the level at which the breeding goal is defined, indicated with P and H respectively. The genotype x environment interaction between the different levels is represented by r_G, while r_{gH} and r_{gP} represent the genotype x environment interaction within the level of the breeding programme, where respectively the breeding goal and index are defined. The aggregate genotype (H) is again defined as the suitabilitity of each genotype on an average fattening herd. In case of selection on own performance only, the performance (OP) of a potential breeding animal is measured under certain environmental conditions, with $var(OP) = \sigma^2_{PP}$, $var(H) = r_{gH} h^2 \sigma^2_{PH}$ and $cov(OP,H) = a r_G h_P h_H \sigma_{PP} \sigma_{PH}$.
The accuracy of selection across levels of the breeding programme on basis of own performance ($r_{IH}(OP)$) then becomes:

$$r_{IH}(OP) = r_G h_P / (r_{gH})^{\frac{1}{2}} \quad (8)$$

In case of progeny or sib information from breeding goal animals, the variance of this information is equal to (1). Further $cov(P,H) = a r_G h_I h_H \sigma_{PP} \sigma_{PH}$ The accuracy of selection on this information across levels of the programme ($r_{IH}(N)$) becomes then:

$$r_{IH}(N) = \left[\frac{a^2 r_G^2 h_P^2 Nmn}{(1+(n-1)(0.5h_P^2+c_P^2)+n(m-1)0.25h_P^2+nm(N-1)0.25h_P^2 r_{gP}) * r_{gH}} \right]^{\frac{1}{2}} \quad (9)$$

The maximum accuracy will be reached with sib or progeny information out of a large number of herds ($N \to \infty$). In that case the variance of the index information becomes $var(P) = 0.25 r_{gP} h^2 \sigma^2_{PP}$. So the maximum accuracy of selection on basis of progeny or half sib information ($r_{IH}(max)$) is:

$$r_{IH}\ (max) = \left[\frac{4a^2 r_G^2}{r_{gP} * r_{gH}} \right]^{\frac{1}{2}} \quad (10)$$

The genetic progress from selection across levels of the breeding programme for the general situation is equal to:

$$\Delta G = i * \left[\frac{a^2 r_G^2 h_P^2 h_H^2 \sigma^2_{PH}\ Nmn}{(1+(n-1)(0.5h_P^2+c_P^2) + n(m-1)0.25h_P^2 + nm(N-1)0.25h_P^2 r_{gP})} \right]^{\frac{1}{2}} \quad (11)$$

SUMMARY

A pig breeding programme generally consists of different levels in a pyramidal structure, indicated as nucleus, multiplication and commercial level. Selection takes place at all levels but improvements generated in the nucleus determine eventually the rate of annual genetic change. Selection at nucleus level for growth and carcass traits is generally based upon performance testing, sometimes supplemented with sib information. These tests usually take place under standardized environmental conditions to allow a fair comparison of the tested pigs. However, these sophisticated conditions may deviate from the conditions at the multiplication level and certainly also from the conditions at commercial fattening where the breeding goal is defined. As a consequence changes in rank order for genotypes between these environments may occur and lower the efficiency of pig breeding programmes. These changes in rank order of genotypes between environments are indicated as genotype x environment interaction (G x E). The size of G x E may be represented by the genetic correlation between the genotypic values of the trait in different environments.

At the end of the 1970's several non-unit estimates of genetic correlations between the different levels of pig breeding programmes were reported in the literature. These results were considered as serious indications of G x E in pig breeding programmes, that might have serious drawbacks for the Dutch pig industry, e.g. for the Dutch herdbook breeding programme in which three levels can be distinguished; nucleus herds with testing at central stations, multiplication herds with on-farm testing and commercial herds with fattening pigs. This encouraged further research into the Dutch herdbook breeding programme on cause and effect of G x E.

The first main object of the project was the investigation of environmental effects in central test, on-farm test and commercial fattening results and the estimation of up-to-date genetic parameters for the traits measured at these levels of the breeding programme. The analyses of G x E may give biased results in case the appropriate definition of environmental effects and up-to-date genetic parameters are not used. Routinely collected central test and on-farm test data from Dutch Landrace (NL) and Dutch Yorkshire (GY) pigs tested between 1979 and 1983 were used. The fattening data of crossbred pigs

were obtained in a progeny test on commercial fattening herds of 65 central and 42 on-farm tested GY-AI-boars.

To investigate the environmental effects within test stations (Chapter 2), different definitions of environmental effects were included separately in models for analysis of variance. Batch effects were significant ($P < 0.001$) for daily gain on test and feed conversion ratio, month effects were significant ($P < 0.05$) for backfat measurements and ham + loin %. Indications for an optimal classification of the environmental effects were shown only for daily gain and feed conversion ratio. For the carcass characteristics no balance could be found between chance and environmental fluctuations. The estimated heritabilities in central test for daily gain on test, feed conversion ratio and ultrasonic backfat thickness were 0.22, 0.23, 0.26 for NL and 0.14, 0.19, 0.29 for GY respectively. Differences between the two breeds in heritabilities were reported, especially for ham + loin % (NL, $h^2 = 0.34$; GY, $h^2 = 0.75$), which may be the result of the selection against halothane-positive animals in NL.

Herd effects were an important source of environmental variation in on-farm test results (Chapter 3) and explained 9 to 20 % of the variance within herdbook regions. A part of these herd effects was due to differences in use of AI-boars between herds. Within herdbook regions these differences were small owing to intensive use of AI. However, across regions indications were found for moderate genetic herd differences. The estimated heritabilities for weight corrected for age, backfat thickness corrected for weight and the performance index were 0.13, 0.39, 0.26 for NL and 0.19, 0.27, 0.22 for GY respectively.

Also in the commercial fattening data (Chapter 5), herd effects were an important source of environmental variation next to seasonal effects. The heritability estimates for daily gain during the fattening period, daily gain during life, the score for backfat thickness and the score for type were 0.05, 0.08, 0.10 and 0.10 respectively. Also carcass weight was analysed and had next to a heritability of 0.05, also a high genetic correlation with the two growth traits.

From these results it was concluded that the evaluation of central and on-farm test results may be improved by an appropriate correction for batch or month effects in central test and for herd effects in on-farm test. Moreover,

the genetic parameters used for these evaluation procedures should be replaced by the estimates reported, especially for the evaluation of NL in central test. In commercial fattening data genetic variance was present but the heritabilities were low if compared to the heritabilities for similar traits in central or on-farm test.

The second main object of the project was the analysis of G x E. The problem of G x E was analysed as (1) the genetic correlations (r_G) between identical traits measured in the nucleus, multiplication and commercial fattening level and (2) the genetic correlations (r_g) among identical traits measured in the various environments within each of the three levels. The data used were the same as in the first part of the project.

Because the traits used in the different levels of the breeding programmes are not identical, genetic correlations between the various definitions of both growth rate and carcass quality were estimated on the basis of central test data (Chapter 1). The genetic correlations between different definitions of growth rate were all close to one (r_g = 0.81 - 1.0). However, the genetic correlations between different definitions of carcass quality (e.g. carcass backfat thickness, ultrasonic backfat thickness and the score for carcass backfat thickness) clearly showed differences in genetic background which should be taken into account in the comparison of these traits across levels of the breeding programme.

In central test results (Chapter 1) sire x batch and sire x month interactions were not significant ($P > 0.05$) for the traits included in the selection; the genetic correlations within the nucleus level (r_{gI}) were equal to one. In on-farm test data (Chapter 4), the sire x herd interaction was significant ($P < 0.001$) for all test characteristics and explained a large part of the total variance. The genetic correlations between sires' progeny performance in different multiplication herds (r_{gII}) varied between 0.3 and 0.7 for weight corrected for age (SC W) and between 0.6 and 0.9 for backfat thickness corrected for weight (SC UB). Non-random mating, preferential treatment of pigs and environment-specific genes are discussed as possible causes of these sire x herd interactions.

At the level of commercial fattening (Chapter 5) the sire x herd interaction was significant ($P < 0.001$) for the growth traits but not for the carcass characteristics. Genetic correlations between sires' progeny performance in

different fattening herds (r_{gIII}) were 0.29 for daily gain during the fattening period and 0.52 for daily gain during life. As there are so many environmental differences between fattening herds, environment-specific genes are expected to be responsible for the low genetic correlations among herds.

The genetic correlations between the different levels of the breeding programme (Chapter 6) were derived from the correlations between best linear unbiased predictions of breeding values at the different levels. Moderate genetic correlations were calculated between central and on-farm test; for backfat thickness r_{G1} = 0.3 -.7, for daily gain r_{G1} = 0.3 - 0.65. Differences in definition of the traits and differences in sex of the progeny were only partly responsible for the moderate relationships. For identical traits measured in central and on-farm test on progeny of the same sex r_{G1} = 0.41 for daily gain and r_{G1} = 0.70 for backfat thickness. Sire x herd interaction in on-farm test data was found to be the responsible factor for the moderate correlations between central test and on-farm test.

Between progeny results in commercial fattening and performances of the sires in central test no clear relationship was found for daily gain, r_{G2} = -0.48 - 0.17, but high correlations for identical carcass characteristics, r_{G2} = 0.57 - 0.64. These results agreed closely with the presence of sire x herd interactions in commercial fattening for only daily gain. The genetic correlations between on-farm test and commercial fattening were high for daily gain, $r_{G3} \cong 1.0$, but low for carcass characteristics, $r_{G3} \cong 0$. The presence of sire x herd interaction in both levels of the breeding programme may be responsible for these inconsistent relationships.

From the analyses of G x E within and between levels of the breeding programme it was concluded that there exist moderate genetic relationships between the different levels of the Dutch herdbook breeding programme. The sire x herd interactions within multiplication and commercial fattening levels are responsible for this. Since the differences between herds, multiplication as well as commercial fattening herds, are numerous and sometimes undefinable, selection of genotypes for suitability under commercial fattening conditions is desirable.

Finally, the consequences of the moderate genetic correlations for the design and efficiency of pig breeding programmes were investigated (Chapter 7).

In general, the accuracy of selection across levels of the breeding programme is directly proportional to $(r_G/[r_{gP} * r_{gH}]^{\frac{1}{2}})$ where r_{gP} and r_{gH} are the genetic correlations within respectively the level where the index information is collected and the level where the breeding goal is defined. However, for a fixed r_G, the highest genetic progress may be reached if $r_{gP} = r_G$. A limited number of test places are best used by distributing the representatives of the genotype over as many herds as possible. The size of r_G in comparison with r_g is discussed further as this has a large impact on the efficiency of the breeding programmes.

Furthermore, some testing strategies were compared for their expected genetic progress with values for r_g and r_G as reported in the different chapters. It was concluded that in general testing of boars and their paternal half sibs in on-farm test or commercial fattening simultaneously is depending on the genetic correlations almost three times more efficient than central testing only. Also two-stage selection with progeny testing in commercial fattening appeared an efficient alternative (1.5 - 2.25 times more efficient than central testing only) under the circumstances of G x E.

SAMENVATTING

Varkensfokprogramma's worden gekenmerkt door een gelaagde opbouw waarin 3 niveaus onderscheiden kunnen worden: topfokkerij, subfokkerij en vermeerdering/mesterij. Deze structuur is duidelijk aanwezig in de fokprogramma's van de fokkerijgroeperingen, maar enigszins verborgen in de opzet van het stamboekfokprogramma omdat daarin topfok- en subfokbedrijven vaak dezelfde zijn. Binnen deze structuur wordt op elk niveau in meer of mindere mate geselecteerd op de economisch belangrijke kenmerken. Echter alleen de selectie op het topfokniveau bepaalt uiteindelijk de genetische vooruitgang van het fokprogramma.

De selectie voor verbetering van de mest- en slachteigenschappen is in het algemeen gebaseerd op prestatie-onderzoek op de selectiemesterij of in de toetsstallen van de fokkerijgroeperingen. Hierbij worden de toetsomstandigheden zoveel mogelijk gestandaardiseerd om een eerlijke vergelijking van de toetsvarkens mogelijk te maken. Deze gestandaardiseerde omstandigheden wijken echter af van de omstandigheden die gelden op subfok- of mesterijniveau. Indien deze verschillen in omstandigheden van invloed zijn op de rangorde van de beren, dan kan de effectiviteit van varkensfokprogramma's daardoor sterk verminderen.

Aan het eind van de jaren zeventig kwam uit diverse onderzoekingen in binnen- en buitenland naar voren dat de verbanden tussen de prestaties onder toetsomstandigheden en onder praktijkomstandigheden aanzienlijk lager zouden zijn dan theoretisch verwacht mag worden. Dit zou betekenen dat er genotype x milieu interacties bestaan die ook in Nederland gevolgen kunnen hebben voor de efficiëntie van varkensfokprogramma's en daarmee voor de kwaliteit van het Nederlandse varken op langere termijn. Daarom werd een onderzoek opgestart met als doel na te gaan wat de mogelijke oorzaken van deze tegenvallende verbanden zijn en op welke wijze deze verbeterd kunnen worden. Hiervoor werd de effectiviteit van de bestaande fokwaardeschattingsprocedures eerst nader onderzocht. Op basis van efficiënte schattingsprocedures werd daarna de aanwezigheid van genotype x milieu interacties geïnventariseerd. Tot slot werden de gevolgen voor de opzet van varkensfokprogramma's uitgewerkt. Voor dit onderzoek werden gegevens uit het stamboekfokprogramma gebruikt omdat deze het meest representatief zijn voor de Nederlandse varkensfokkerij. Hierbij is er vanuitgegaan dat de topfokkerij op basis van selectiemesterijgegevens bedreven wordt en dat de bedrijfsprestatietoets alleen ten dienste staat van de subfokkerij.

Genetische parameters en storende invloeden bij het schatten van fokwaarden

De eerste hoofdlijn in het project betrof het onderzoek naar de optimalisatie van de fokwaardeschatting op basis van selectiemesterij- en bedrijfsprestatietoetsgegevens en het schatten van genetische parameters voor op de selectiemesterij, in de bedrijfsprestatietoets, en op mesterijbedrijven gemeten kenmerken. Alleen indien er zekerheid bestaat omtrent de juistheid van de procedures in topfok- en subfokniveau en men de juiste genetische parameters kent, is een zinvolle bestudering van genotype x milieu interactie mogelijk. Selectiemesterij- (SM) en bedrijfsprestatietoets- (BPT) gegevens van Groot Yorkshire (GY) en Nederlands Landvarken (NL) verzameld vanaf 1979 tot en met 1984 werden geanalyseerd. In totaal betrof dit de gegevens afkomstig van 136.444 varkens. Voor de verzameling van individuele mesterijgegevens werd een nakomelingenonderzoek van GY-KI-beren opgezet in samenwerking met de Varkens-KI-Vught, de Integratiedienst van de Vee- en Vleescentrale van de NCB en 27 vermeerderingsbedrijven. Van deze GY-KI-beren hadden er respectievelijk 65 en 42 een eigen prestatie op de selectiemesterij en in de bedrijfsprestatietoets. Dit resulteerde in individuele gegevens van 8148 mestvarkens, gemest op 35 mestbedrijven.

In hoofdstuk 2 werd voor de SM-gegevens nagegaan voor welke storende milieu-invloeden de verschillende kenmerken gecorrigeerd moeten worden. Geconstateerd werd dat groei en voederconversie gecorrigeerd moeten worden voor groepseffecten, waarbij een groep gedefinieerd is als de varkens welke tegelijkertijd binnen een afdeling getoetst worden. Voor spekdiktemetingen en ham + karbonade % leverde een correctie voor maandeffecten het beste resultaat. De geschatte erfelijkheidsgraden voor groei, voederconversie en ultrasone spekdikte waren respectievelijk 0,22, 0,23, 0,26 voor NL en 0,14, 0,19, 0,29 voor GY. Voor ham + karbonade % werd een groot verschil in erfelijkheidsgraad tussen NL en GY geconstateerd (resp. h^2 = 0,34 en 0.75), dat mogelijk toe te schrijven is aan de selectie tegen halothaanovergevoeligheid binnen het NL-ras.

Bij de analyse van de BPT-resultaten (hoofdstuk 3) bleken met name de bedrijfsverschillen van grote betekenis. Een deel van deze bedrijfsverschillen dient echter niet als storend aangemerkt te worden. Binnen de stamboekregio's bleek 5 tot 18 % van de bedrijfsverschillen in de index voort te komen uit verschillen in gebruikte KI-beren. Over regio's heen waren de beergebonden be-

drijfsverschillen groter, waarschijnlijk als gevolg van een beperkte uitwisseling van KI-beren tussen de stamboekregio's. De geschatte erfelijkheidsgraden voor het toetsgewicht gecorrigeerd voor leeftijd (score voor gewicht), ultrasone spekdikte gecorrigeerd voor gewicht (score voor spekdikte) en de index waren respectievelijk 0,13, 0,39, 0,26 voor NL en 0,19, 0,27 en 0,22 voor GY.

In hoofdstuk 5 bleek dat ook in de mesterijresultaten bedrijven de belangrijkste storende invloed vormden naast seizoenseffecten. De erfelijkheidsgraden voor mesterijgroei, levensgroei, spekdikte- en typebeoordeling (volgens de oude classificatie) bedroegen respectievelijk 0,05, 0,08, 0,10 en 0,10. Ook geslacht gewicht was als afzonderlijke variabele geanalyseerd, omdat op de meeste mestbedrijven het "all in - all out"-systeem werd toegepast. Voor geslacht gewicht bleek de erfelijkheidsgraad gelijk aan 0,05 en de genetische correlatie met mesterij- en levensgroei nagenoeg gelijk aan 1.

Op basis van deze resultaten is geconcludeerd dat de efficiëntie van het selectiemesterij-onderzoek gebaat is bij een correctie van groei en voederconversie voor groepseffecten en een correctie van karkaskenmerken voor maandeffecten. Om bedrijfsprestatietoetsresultaten over bedrijven heen vergelijkbaar te maken, is correctie voor bedrijfseffecten noodzakelijk. Hierbij moeten de verschillen in genetisch niveau tussen de bedrijven echter intact blijven. De geschatte genetische parameters voor SM- en BPT-resultaten vertoonden verschuivingen ten opzichte van de in het verleden geschatte parameters. Deze verschuivingen onderstrepen het belang van onderhoud aan fokwaardeschattingsprocedures. Voor de kenmerken die op de mestbedrijven gemeten werden, was genetische variantie in beperkte mate aanwezig. Bij "all in - all out"-systemen bleek het geslacht gewicht een eenvoudige, maar wel goede indicator voor zowel mesterij- als levensgroei.

De analyse van de genotype x milieu interacties

De tweede hoofdlijn in het project betrof de analyse van genotype x milieu interacties. Hierbij wordt het belang van de interactie uitgedrukt als de genetische correlatie tussen identieke kenmerken gemeten in verschillende milieus. Indien de rangorde van genotypen (bijv. nakomelingengroepen van KI-beren) niet door het milieu beïnvloed wordt, dan wordt een genetische correlatie van 1 verwacht. Bij de analyse werd een onderscheid gemaakt tussen (1)

de genetische correlaties (r_G) tussen identieke kenmerken gemeten in de selectiemesterij, bij de bedrijfsprestatietoets en op mestbedrijven en (2) de genetische correlaties (r_g) tussen identieke kenmerken gemeten in de verschillende milieus (bijv. bedrijven) binnen één van de drie niveaus in het fokprogramma. Voor het schatten van deze correlaties zijn dezelfde gegevens gebruikt als in het eerste deel van het project.

Het schatten van de genetische correlaties (r_G) tussen kenmerken gemeten in de verschillende niveaus in het fokprogramma, kan alleen een goede indicatie zijn voor genotype x milieu interactie als identieke kenmerken gecorreleerd worden. Daarom zijn in hoofdstuk 1 de verschillende definities voor groei en voor slachtkwaliteit die in het algemeen gehanteerd worden, eerst onderling vergeleken aan de hand van selectiemesterijgegevens. Het bleek dat de genetische correlaties tussen toetsgroei (25 - 100 kg), levensgroei (geboorte - 100 kg) en mesterijgroei (aankomst meststal - 100 kg) hoog zijn (0,81 - 1,0). Echter de genetische correlatie tussen ultrasone spekdikte en rugspekdikte was gelijk aan 0,6 en de correlatie van elk van deze spekdiktemetingen met de spekdiktebeoordeling bij de classificatie gelijk aan respectievelijk 0,3 en 0,8. Het meten van de ultrasone- of rugspekdikte bleek daarnaast een beperkte voorspellende waarde voor het ham + karbonade % te hebben. Met deze verschillen in definitie voor groei en voor slachtkwaliteit moet derhalve rekening gehouden worden bij het schatten van r_G.

In hoofdstuk 1 bleek verder dat bij selectiemesterijresultaten de rangorde van nakomelinggroepen van vaders niet beïnvloed werd door groeps- of maandeffecten. Vader x groep of vader x maand interacties waren statistisch niet aantoonbaar: $r_g = 1$. Echter in hoofdstuk 4 bleek dat voor de bedrijfsprestatietoetskenmerken de rangorde van nakomelinggroepen bedrijfsafhankelijk was; de vader x bedrijf interactie was significant ($P < 0,001$). De genetische correlatie tussen nakomelinggroepen van KI-beren in verschillende bedrijven varieerde tussen 0,3 en 0,7 voor gewicht gecorrigeerd voor leeftijd, tussen 0,6 en 0,9 voor spekdikte gecorrigeerd voor gewicht en tussen 0,5 en 0,7 voor de index. Mogelijke oorzaken voor deze interacties als gerichte paringen en voorkeursbehandeling van bepaalde varkens zijn bediscussieerd. Gezien echter de grote verschillen in omstandigheden tussen de bedrijven moet de oorzaak met name in bedrijfsspecifieke genen gezocht worden; de expressie van de genetische aanleg wordt dan gedeeltelijk bepaald door de (bedrijfs)omstandigheden.

In hoofdstuk 5 bleek dat voor de mesterijgegevens de vader x bedrijf inter-

actie eveneens duidelijk aanwezig was ($P < 0,001$) voor mesterij- en levensgroei, echter niet voor de spekdikte- en typebeoordeling ($P > 0,05$). De genetische correlatie tussen nakomelinggroepen van KI-beren in verschillende bedrijven was 0,29 voor mesterijgroei en 0,52 voor levensgroei. Deze interacties kunnen nagenoeg alleen voortkomen uit bedrijfsspecifieke genen.

In hoofdstuk 6 zijn de genetische correlaties tussen de verschillende niveaus in het fokprogramma (r_G)afgeleid uit de correlaties tussen fokwaarden voor vaders in elk van deze niveaus, geschat m.b.v. de Best Linear Unbiased Prediction (BLUP)methode. Hierbij zijn de gegevens gecorrigeerd voor de storende invloeden welke in het eerste deel van het project gerapporteerd zijn. De genetische correlaties tussen kenmerken gemeten op SM en BPT bedroegen voor spekdikte $r_{G1} = 0,3 - 0,7$, voor groei $r_{G1} = 0,3 - 0,65$. Verschillen in definitie tussen SM- en BPT-kenmerken zijn, evenals verschillen in sexe tussen nakomelingengroepen, slechts voor een beperkt deel verantwoordelijk voor deze matige correlaties. Voor levensgroei en ultrasone spekdikte gemeten aan alleen beertjes op SM en bij BPT waren de genetische correlaties (r_{G1}) gelijk aan respectievelijk 0,41 en 0,70. Deze matige correlaties, de theoretisch verwachte correlatie is gelijk aan 1, lijken het gevolg van de gerapporteerde vader x bedrijf interactie in de BPT-resultaten.

Tussen de nakomelingenresultaten in de mesterij en de eigenprestatie van de vaders op de selectiemesterij werd geen duidelijk verband gevonden voor groei ($r_{G2} = -0,48 - 0,17$), maar wel voor de classificatieresultaten ($r_{G2} = 0,57 - 0,64$). Deze resultaten komen overeen met het bestaan van vader x bedrijf interactie in de mesterijgegevens voor alleen groei. De genetische correlaties tussen de eigenprestaties van KI-beren in de BPT en de nakomelingenresultaten in de mesterij waren hoog voor groei, $r_{G3} \cong 1$, maar laag voor de slachtkenmerken $r_{G3} \cong 0$. De aanwezigheid van vader x bedrijf interacties in beide niveaus (BPT en mesterij) wordt verantwoordelijk geacht voor de verschillen in correlaties voor groei en slachtkwaliteit.

Deze resultaten getuigen van het bestaan van aanmerkelijk lagere verbanden tussen de verschillende niveaus in het fokprogramma dan theoretisch verwacht mag worden. Vooral de matige verbanden met de mesterijresultaten hebben een grote invloed op de efficiëntie van de huidige fokprogramma's. De genetische vooruitgang voor mest- en slachteigenschappen moet daarbij namelijk voortkomen uit de selectie op basis van alleen resultaten op topfokniveau. De oorzaak van

deze matige verbanden moet niet zozeer gezocht worden in het niet- optimaal zijn van de omstandigheden op topfokniveau, maar meer in het bestaan van vader x bedrijf interacties op subfok- en mesterijniveau. Daardoor kunnen de verbanden tussen de verschillende niveaus in het fokprogramma niet beter zijn dan de onderlinge verbanden tussen praktijkbedrijven. Verbetering van de verbanden tussen de verschillende niveaus moet dan ook voortkomen uit meer inzicht in de factoren die de hoogte en variatie van de genetische correlaties tussen bedrijven bepalen. Echter, de verschillen in omstandigheden tussen praktijkbedrijven zijn groot en vaak zelfs zo ondefinieerbaar, dat het noodzakelijk wordt de fokprogramma's om te buigen naar selectie op geschiktheid onder alle voorkomende praktijkomstandigheden.

Gevolgen voor varkensfokprogramma's

Tot slot zijn in hoofdstuk 7 de gevolgen van de matige genetische relaties binnen en tussen niveaus in het fokprogramma nader bestudeerd, met name voor de opzet en de efficiëntie van varkensfokprogramma's. Uit theoretische afleidingen kwam vast te staan dat met een beperkt aantal toetsplaatsen op verschillende bedrijven efficiënt omgesprongen wordt, wanneer de nakomelingen van een vader over zoveel mogelijk bedrijven verspreid worden. Voorts is het belang van de correlatie tussen niveaus (r_G) ten opzichte van de correlatie binnen niveaus (r_g) nader uitgewerkt voor de nauwkeurigheid van selectie en de genetische vooruitgang. De genetische vooruitgang bleek duidelijk positief beinvloed te worden door hogere genetische correlaties tussen nakomelinggroepen van vaders op verschillende mestbedrijven. Met de selectie op topfok- en subfokniveau wordt het beste resultaat behaald wanneer de genetische correlaties tussen elk van deze niveaus en het mesterijniveau gelijk zijn aan de genetische correlaties binnen topfok- en subfokniveau ($r_G = r_g$ (index)).

De geschatte genetische correlaties r_G en r_g voor levensgroei en ultrasone spekdikte zijn gebruikt om de efficiëntie te bepalen van een drietal fokprogramma's. Hieruit bleek dat fokprogramma's waarin tegelijkertijd beren centraal en half broers of zusters in de BPT of op mestbedrijven getoetst worden, veel efficiënter zijn, tot bijna het drievoudige, dan programma's waarin de selectie alleen gebaseerd is op centraal toetsen. Ook fokprogramma's waarin nakomelingenonderzoek op mestbedrijven opgenomen is, zijn efficiënter dan programma's met alleen centraal toetsen. Dit voordeel liep op tot ruim 2 keer de

oorspronkelijke genetische vooruitgang. Dit heeft tot gevolg dat het noodzakelijk is varkensfokprogramma's om te buigen in de richting van selectie op basis van een combinatie van eigenprestatie-onderzoek onder toetsomstandigheden en familie-informatie verkregen onder praktijkomstandigheden.

CURRICULUM VITAE

Jan W.M. Merks werd op 17 maart 1958 geboren te Son en Breugel (Noord-Brabant), waar hij ook opgroeide op een veehouderijbedrijf. In 1976 behaalde hij het Atheneum-B-diploma aan het Eckart College te Eindhoven. In datzelfde jaar begon hij met zijn studie Zoötechniek aan de Landbouwuniversiteit te Wageningen. Deze studie werd op 1 februari 1982 afgesloten met als verzwaard hoofdvak de Veeteelt en als bijvakken de Dierfysiologie en de Algemene Agrarische Economie. Na zijn afstuderen werd hij aangesteld als wetenschappelijk medewerker in tijdelijke dienst bij de Vakgroep Veefokkerij der Landbouwuniversiteit en gedetacheerd bij het Instituut voor Veeteeltkundig Onderzoek "Schoonoord" te Zeist. Sinds 1 juli 1984 is hij als wetenschappelijk medewerker op het gebied van de Varkensfokkerij werkzaam bij laatstgenoemd Instituut.