Studies on breeding schemes in a closed pig population

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Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C. C. Oosterlee,
in het openbaar te verdedigen
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des namiddags te twee uur in de aula
van de Landbouwuniversiteit te Wageningen.

STELLINGEN

1. De genetische vooruitgang kan worden gemaximaliseerd door scherpe selectie te combineren met het gebruik van een zodanig aantal mannelijke fokdieren, dat de genetische variabiliteit op een redelijk peil blijft.
   Dit proefschrift.

2. De genetische vooruitgang wordt overschat, wanneer geen rekening gehouden wordt met de afname van de genetische variantie ten gevolge van selectie.
   Bulmer, M.G. (1971). The effect of selection on genetic variability. Am. Nat. 105: 201-211.
   Dit proefschrift.

3. Landbouwhuisdierpopulaties lijken vaak groot, maar zijn in genetische zin meestal klein door het intensieve gebruik van een klein aantal verwante mannelijke fokdieren.

4. Foktechnisch gezien is inteelttoename vooral van belang, omdat het de genetische variantie doet afnemen en minder vanwege de directe en indirecte effecten van inteeltdepressie.
   Dit proefschrift.

5. Fokwaardeschattingen zijn onzuiver, wanneer deze zijn gebaseerd op gegevens van dieren die verschillen in inteeltcoëfficiënt en wanneer er bovendien sprake is van dominantie.
   Kennedy, B.W. and Sörensen, D.A. (1988). Properties of mixed model methods for prediction of genetic merit. (in preparation).
   Dit proefschrift.

6. Maximale inteeltvermijding levert in termen van minimalisatie van de inteelttoename nauwelijks voordelen op ten opzichte van een simpeler paringssysteem, waarbij slechts het paren van nauwe verwanten wordt voorkomen.
   Robertson, A. (1964). The effect of non-random mating within inbred lines on the rate of inbreeding. Genet. Res. 5: 164-167.
   Dit proefschrift.

7. Het zou in de fokkerij minder normaal moeten zijn om een kenmerk als normaal verdeeld te beschouwen.

8. Klonering is voor "echte" fokkers niet interessant, het is immers niet anders dan het consolideren van de status quo.

9. Net als in de politiek is het in de rundveefokkerij niet gezond als slechts enkele toppers de lakens uitdelen.

10. Een opmerkelijke overeenkomst tussen het lopen van een marathon en het uitvoeren van fokprogramma is dat men in het begin niet al zijn kruit moet verschieten.

11. Teveel mest leidt tot verzuring van de bossen, een teveel aan regels leidt tot verzuring van de boeren.

12. Oostindische doofheid is een ernstige kwaal, die de leefbaarheid van de samenleving van slaapkamer tot Tweede Kamer negatief beïnvloedt.

13. De nacht gaat over in de dag, zodra je in de ogen van een ander je broer of zuster herkent.
    Joodse rabbi.

Proefschrift van G. de Roo
Studies on breeding schemes in a closed pig population
Wageningen, 19 februari 1988.

Aan mijn ouders
Aan Greetje en Margriet

De Roo, G., 1988. Studies on breeding schemes in a closed pig population (Onderzoek naar fokprogramma's voor een gesloten varkenspopulatie). Doctoral thesis, Department of Animal Breeding, Agricultural University, Wageningen, The Netherlands.

VOORWOORD

Het in dit proefschrift beschreven onderzoek is uitgevoerd in het kader van een promotie-assistentschap bij de vakgroep Veefokkerij van de Landbouwuniversiteit te Wageningen. Een flink aantal mensen heeft bijgedragen aan de voortgang van het onderzoek. Voor alle grote en kleinere bijdragen: hartelijk dank!

Mijn promotor prof. dr. ir. R.D. Politiek dank ik voor de mij geboden mogelijkheid om dit onderzoek te doen. Uw stimulerende belangstelling en uw bijdragen in de besprekingen heb ik zeer op prijs gesteld. Mijn co-promotor dr. ir. Hein van der Steen heeft menigmaal als klankbord gefungeerd. Je inzicht en ervaring zorgden voor een goede weerklank.

De discussies in de leescommissie zijn voor mij erg waardevol geweest. Johan van Arendonk, Egbert Kanis en Alfred de Vries: hartelijk dank! Wiebe Koops, jouw ervaring en inzicht in het werken met modellen waren voor mij bijzonder stimulerend.

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CONTENTS

Chapter 1

INTRODUCTION

Size of a population in genetic terms is a function of number of male and female individuals used for breeding over a generation (Wright, 1931). A breed, therefore, can be small because of a small total number of individuals but also because of a small number of individuals of one sex. According to this definition, many breeds of livestock, pets and zoo animals are small populations.

Total number of individuals, for example, may be small because of historical reasons (diseases, low popularity of the breed) or because of a limited actual economic importance of the breed. Genetic conservation of such a breed is thought important because its genetic material could be valuable for future production requirements or because its economic importance is not yet identified as such (Maijala et al., 1984).

A breed that seems to be large can in fact be small because few animals are selected for breeding. Techniques like artificial insemination and embryo transfer facilitate concentration on few, highly selected breeding animals. The breeding scheme applied in such a situation often involves use of a nucleus, in which genetically superior animals are gathered (e.g. James, 1977). Development of different lines for specific purposes is common in poultry and pig breeding and is considered desirable in horse breeding (Langlois et al., 1983). A nucleus structure is promoted in sheep and goat breeding (Nicoll et al., 1986) and its potential has been investigated by dairy cattle breeders (Hinks, 1974; Nicholas and Smith, 1983).

A breeding scheme designed for such a finite population should lead to continuous genetic improvement over a period of time of interest to breeders. Available additive genetic variance, therefore, should be used efficiently. This is not straightforward because selection in one generation affects the additive genetic variance in the next generation (Bulmer, 1971, 1976). Moreover, generations overlap and selection of animals is a continuous process. Another complication is the increase in additive genetic relationship between animals, which leads to the mating of relatives ('inbreeding') and is inevitable in a finite population. Inbreeding reduces the additive genetic variance available for selection and, secondly, has a negative effect on the mean of traits subject to dominance (Falconer, 1981).

Simple formulae for the prediction of selection response, that take account of these complications, do not exist (Hill, 1977).

The aim of this thesis was optimization of breeding schemes in finite populations. Attention was focussed on breeding schemes in a closed swine herd as an example of a finite population in which both selection and inbreeding are relevant. The outcome of a breeding scheme for such a herd is affected by many factors as, for example, population size and structure, founder population size and selection and mating strategies. The effects of variation in a number of these factors on selection response and rate of increase in the inbreeding coefficient (F) were studied.

In this chapter, the method followed is highlighted, with special attention on the design of the breeding scheme and on the genetic model assumed.

1. METHOD

Replicated experimentation with livestock is costly and time consuming. Knowledge of inheritance of traits and of interactions between factors included in the breeding scheme can be increased by means of laboratory animal modelling and computer modelling (e.g. Robertson, 1980; Roberts, 1982; Harris and Stewart, 1986). The validity of results of model studies depends on the accuracy of modelling. Results from experiments with Drosophila, Tribolium or mice (e.g. Hammond, 1974; Eisen, 1980; Enfield, 1980; Frankham, 1982) can not be used directly in a breeding program for, for example, cattle or swine, but contribute significantly to the understanding of inheritance of traits (Roberts, 1982).

Present available computer facilities enable the building of computer models that reflect the practical breeding situation closely. This research requires a thorough analysis of the system to be modelled. Such an analysis can clarify which parts of the system need further experimental attention.

A combination of experiments with the species of interest and different types of modelling is needed in a systematic analysis of breeding programs (Harris and Stewart, 1986). The type of modelling used in a specific study depends on its purpose. Computer modelling is especially useful when questions raised are complicated (Robertson, 1980).

1.1 Design of the breeding program

Optimization of breeding schemes requires a systematic approach to their design. Harris et al. (1984) distinguished nine steps:

1 description of the production system,
2 formulation of the objective of the system,
3 choice of breeding system (pure breeding/cross breeding) and breeds,
4 estimation of selection parameters and economic weights,
5 the design of an animal evaluation system,
6 development of selection criteria,
7 the design of mating of selected animals,
8 the design of a system for expansion,
9 comparison of alternative programs.

These steps served as a starting point in this study. Attention was focussed on breeding in a nucleus herd, a system for expansion was not contemplated. The first seven steps were considered in the building of a model of a nucleus herd that is described in the first chapter, the other chapters deal with the comparison of alternative programs.

1.2 Genetic model

Chance plays an important role in small populations. Replicated experiments with the same breeding program can lead to quite different results (e.g. Pirchner, 1985). With a Monte Carlo approach mean results of a breeding scheme and variability of this mean can be studied (Brascamp, 1978). A model with random deviates (Kennedy and Gentle, 1980), therefore, is more appropriate than a deterministic model.

The genetic model describes the inheritance of traits. It can be designed at the locus level or at the animal level. A model designed at the locus level is especially useful for the purpose of studying different ways of inheritance of traits. Genetic models that include additive and dominance effects, different degrees of linkage and recombination and epistatic effects can be studied. Number of possible genetic models becomes numerous when number of loci increases. Many studies have been undertaken to clarify the effect of specific genetic models (Gill, 1965; Quereshi and Kempthorne, 1968; Bereskin et al., 1969; Parker et al., 1969; Robertson, 1970, 1977; Davis and Brinks, 1983; Mueller and James, 1983). Robertson (1970) stated that even for a relative simple genetic model of additive effects and initial linkage equilibrium, seven parameters are required to describe the initial state of the population and the selection process:

- effective population size (N),
- number of loci (n),
- the difference between two homozygotes at each locus (a),
- the initial frequency of the desirable allele at each locus (q),
- the intensity of selection (i),
- the phenotypic variance of the character (σ_p),
- the map distance between adjacent loci (l).

This approach assumes only two possible alleles at each locus. If this number is larger, the third parameter becomes more complicated and a distribution of gene effects with a certain mean and variance must be chosen for each locus.

The selection policy that will yield best results, depends on the true genetic model. Selection of just the best individuals would be the best selection method if all genes affecting the trait were concentrated on one chromosome and if crossing over would be absent. In that situation, no better can be done than fixing the best chromosome present in the population, because a rearrangement of genes does not occur (Robertson, 1970). Robertson showed that selection of just the best individuals would also be best with free recombination, a low number of loci and high frequencies of desirable genes.

The best genotype that can be created by selection combines all positive genes present in the population. With free recombination, a large number of loci and intermediate frequencies of desirable genes, it is unlikely that all positive genes are present in a few highly selected animals. Robertson (1960) stated, that under an infinitesimal model, the limit of selection was highest when 50 percent of the population was selected for breeding. Optimal selection intensities for mid-term response to selection are unclear.

In many studies, gene effects and frequencies at different loci were assumed to be equal. Hill (1985) suggested use of a joint probability density function, over loci, of gene effects and frequencies. He stated, however, that there was little information on which to base such a density function. Hill (1985) thought an exponential curve, such that many genes have a small effect and only a few a large effect, acceptable. Differences in gene effects or frequencies between loci could modify the optimal selection policy. The larger the differences in gene effect, the stronger the resemblance with the alternative with no crossing over (Robertson, 1970). Robertson thought differences in initial gene frequencies less important than differences in gene effects.

Except for extreme values of the initial gene frequency, the cumulative distribution of gene effects quickly approached normality when number of loci increased (Robertson, 1970). Selection response was a function of N*i*h, where h is the square root of the heritability, and was independent of number of loci and initial gene frequency. Number of parameters needed to characterize the genetic model, thus, was reduced.

A model in which breeding values of traits are simulated by means of normal deviates (e.g. Brascamp, 1978) can be applied when a considerable number of loci affect the trait, with intermediate gene frequencies, small differences in gene effects between loci and no epistasis. If the initial gene frequency of desirable alleles is low, response to selection will be higher than expected from a model with normal deviates with parameters based on the observed genetic variance in the base population. Selection causes an increase in gene frequencies, which is accompanied by a relative large increase in additive genetic variance when initial gene frequencies are low (Falconer, 1981). As soon as gene frequencies reach intermediate levels, however, the model is appropriate, at least when genetic parameters are adapted to the new situation. In a population under selection, genes with large effects or at high frequencies will quickly be fixed. This reduces the additive genetic variance and response to selection will be lower than expected from a model with normal deviates. Further response to selection is to be obtained from the remaining segregating genes, which are at intermediate gene frequencies and have a small effect each. The normal deviate model with adapted genetic parameters is, again, appropriate. Selection may ultimately increase gene frequencies beyond intermediate levels. In that case additive genetic variance and response to selection reduce.

Quantitative traits in pig breeding are assumed to be affected by many loci. Other above mentioned assumptions do not prohibit use of a model with normal deviates. The genetic model to be used, however, should allow for inbreeding. The pedigree inbreeding coefficient (F) is a satisfactory estimate of the degree of homozygosity in livestock species, which have a high proportion of unlinked genes (Weir et al., 1980). The inbreeding coefficient of an animal determines the amount of variation in its gametes, and can, therefore, be used to generate breeding values of offspring:

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{(0.5 * CF)} * a * \sigma_A \qquad (1)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \qquad (2)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,

CF : correction factor that accounts for the expected reduction in additive genetic variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),

a : random normal deviate,

σ_A : additive genetic standard deviation.

Besides the effect of inbreeding on the additive genetic variance it is also expected to have an effect on the mean of traits subject to dominance (Falconer, 1981). Dominance effects are not transmitted intact from parent to offspring because of segregation and recombination. These effects can be regarded as part of the environmental effects when dominance relationships between animals are ignored. With the assumptions of many unlinked loci affecting the trait and equal contributions of loci to the overall dominance effect, inbreeding depression effects are a linear function of F.

Phenotypes can be simulated as

$$P_i = B + A_i + E_i - b_f * F_i \qquad (3)$$

where P_i : phenotypic value,

B : base level,

E_i : random environmental component,

b_f : regression coefficient that reflects the degree of inbreeding depression.

A normal deviate approach, as illustrated by eqs. 1 to 3, is followed in this thesis.

2. CONTENTS OF THE THESIS

This thesis concentrates on breeding programmes in a closed swine herd. Construction of a stochastic model, that measures genetic changes in production and reproduction traits and inbreeding coefficient, is reported in chapter 2. This model is used in subsequent chapters for the evaluation of alternative breeding schemes.

Population size at the nucleus level is an important factor with respect to costs and benefits of pig breeding. Selection response is dependent on number of boars and sows available for selection and on number of each sex used for breeding. Effects of variation in population size on selection response and rate of increase in the inbreeding coefficient are described in chapter 3.

The design of a mating system for selected animals needs special attention (Harris et al., 1984). Mating policy includes the choice whether and to what extent mating of relatives should be avoided. It also implies choice of number of boars to be used simultaneously for breeding. Alternative mating policies are compared in chapter 4.

At the start of a new line in pig nucleus breeding, the question of size of the founder population arises. The founder population should have a high mean breeding value and contain a substantial amount of genetic variation. Effects of changes in size of the founder population, in effective population size after the foundation period and in intensity of selection of founder animals from a base population are evaluated in chapter 5.

An increase in F, which is inevitable in closed, finite populations, causes a reduction in the additive genetic variance available for selection. Such an increase, moreover, causes a decrease in heterozygosity and, thus, in the mean of traits subject to dominance, known as inbreeding depression. Effects of inbreeding depression are ignored in chapters 3 to 5 to avoid confounding of the effects of F on the mean and on the additive genetic variance. The aim of chapter 6 is to study effects of inbreeding depression on selection response and F over time.

Implications of the study for the design of breeding schemes in general and, more specific, for selection in some livestock species are discussed in the final chapter. Effects of opening of the nucleus and breeding programmes that aim at conservation of animal genetic resources are also considered.

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Chapter 2

A STOCHASTIC MODEL TO STUDY BREEDING SCHEMES IN A SMALL PIG POPULATION

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SUMMARY

A stochastic model was constructed to examine the time-course of production and reproduction traits and inbreeding coefficient of a pig nucleus breeding scheme for different population sizes. Traits were simulated at the animal level; week was used as unit of time.

The model includes overlapping generations and continuous selection in boars and sows. Such a model allows the study of effects of population size and structure, size of founder population and different selection and mating systems on selection response and inbreeding coefficient.

As an example, the model is applied to the situation of a sire line with 50 sows and 15 boars annually.

1. INTRODUCTION

Management of small populations, such as a line of chickens or pigs of breeding companies, includes a breeding scheme that exploits available genetic variance efficiently and prevents problems resulting from inbreeding. A variety of factors influence the outcome of a pig nucleus breeding scheme (figure 1).

Theory of breeding schemes often assumes infinite population size and constant variance over generations. In closed, finite populations, however, these assumptions do not hold; drift and selection each has an effect on the mean and on genetic variance for different traits. Genetic theory of long-term response to selection states that a balance must be found between effective population size and selection intensity (Robertson, 1960). The time-span of interest to breeding companies, however, is probably limited to 15 or 20 years. Implications of long-term theory for the practical situation of small pig populations need further investigation.

A number of papers focus attention on one variable from figure 1 by means of an algebraic approach (e.g. Smith, 1969; James, 1970; Robertson, 1970; Dempfle, 1975; James, 1982). Other papers are directed towards more specific pig breeding situations (Fredeen and Martin, 1967; Bereskin et al., 1969; Kemp and Magee, 1970; Hagenbuch and Hill, 1978; McPhee and Macbeth, 1984; Macbeth and McPhee, 1986). Comprehensive models that apply to the commercial level in the production pyramid are designed by Allen and Stewart (1983), Tess et al. (1983) and Singh (1986). An integrated study of the pig

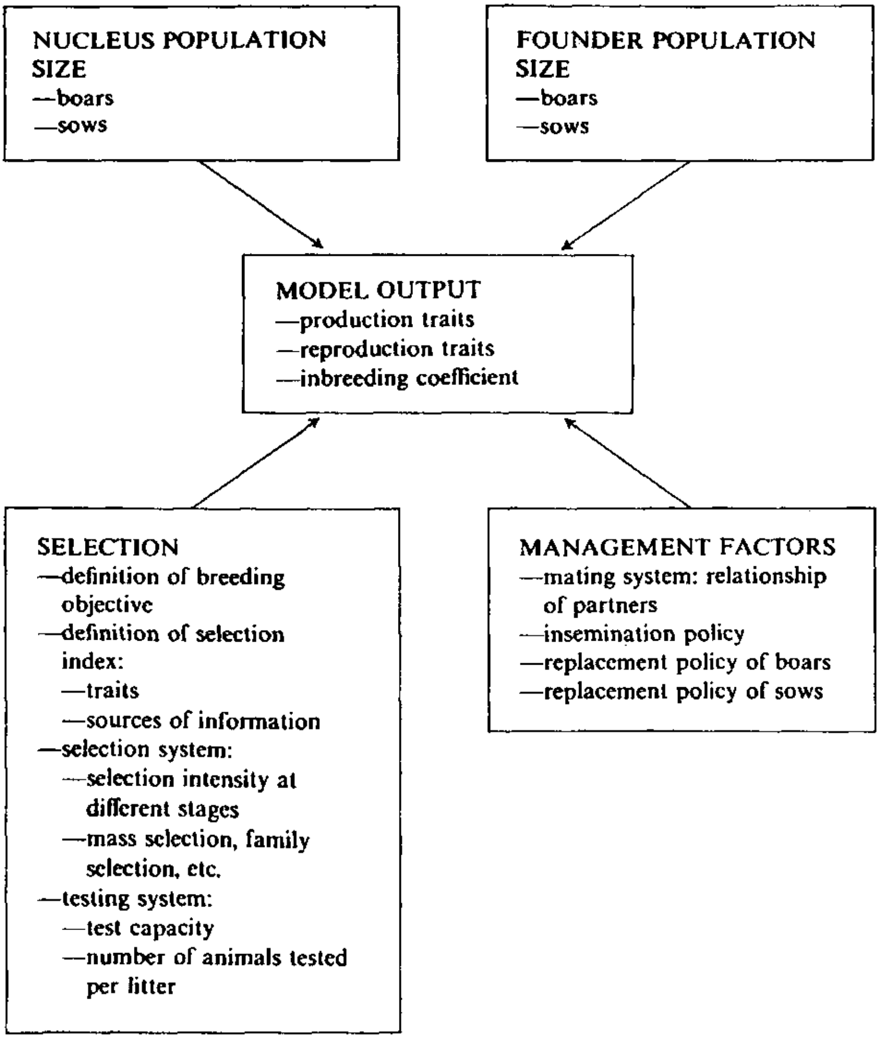

Fig. 1. Schematic representation of variables which affect pig nucleus breeding.

nucleus breeding system, with emphasis on selection and directed towards the practical situation of a breeding company, was not found in the literature.

Pig nucleus breeding includes overlapping generations and continuous selection of boars and sows. Number of animals available for selection at a given moment is often small and number of traits of economic importance is relatively large. From a cost point of view, size of nucleus population and test capacity should be limited.

This paper reports on construction of a stochastic model to examine the time-course of production and reproduction traits and inbreeding coefficient for a pig nucleus breeding situation. As an illustration the model is applied to a sire line.

2. MODEL DESCRIPTION

2.1 General concepts

Breeding companies tend to keep their nuclei as closed lines (Bichard and David, 1984). A closed nucleus would be necessary because of disease prevention. Secondly, it is difficult to buy high quality breeding stock that fits into the breeding scheme. In this paper, possibilities of breeding within a closed line, referred to as nucleus, will be examined.

Chance plays an important role in small populations. One example is weekly selection of boars and sows and its effect on variance and selection response. The effect of chance can not be studied with a deterministic approach. For this reason, Monte Carlo is used in modeling.

The model is designed at the level of the animal. A scheme of the life cycle of animals and reasons for culling that are included in the model, are in figure 2. Every event corresponds to a special pig house (figure 3) and to a certain time-span. In the practical situation many processes, such as selection or transfer of animals to other pig houses, occur just once a week. For this reason, the model is executed weekly.

2.2 Traits in the model

Animals are characterized by their pedigree (sire, dam, inbreeding coefficient), time variables (e.g. date of birth, date of last mating) and production and reproduction traits (table 1). Total number of traits is limited to keep the model manageable.

In The Netherlands, performance test of potential breeding animals plays a central role in the breeding scheme. Dutch breeding organizations generally record growth rate and side-fat thickness for boars and sows. Measurement of individual feed intake, however, is often reserved for boars.

Side-fat thickness, ultrasonically measured 5 cm from the median on the back, is used in index calculations because of its relation with the amount of lean in the body. About fifty percent of the variance in lean content can

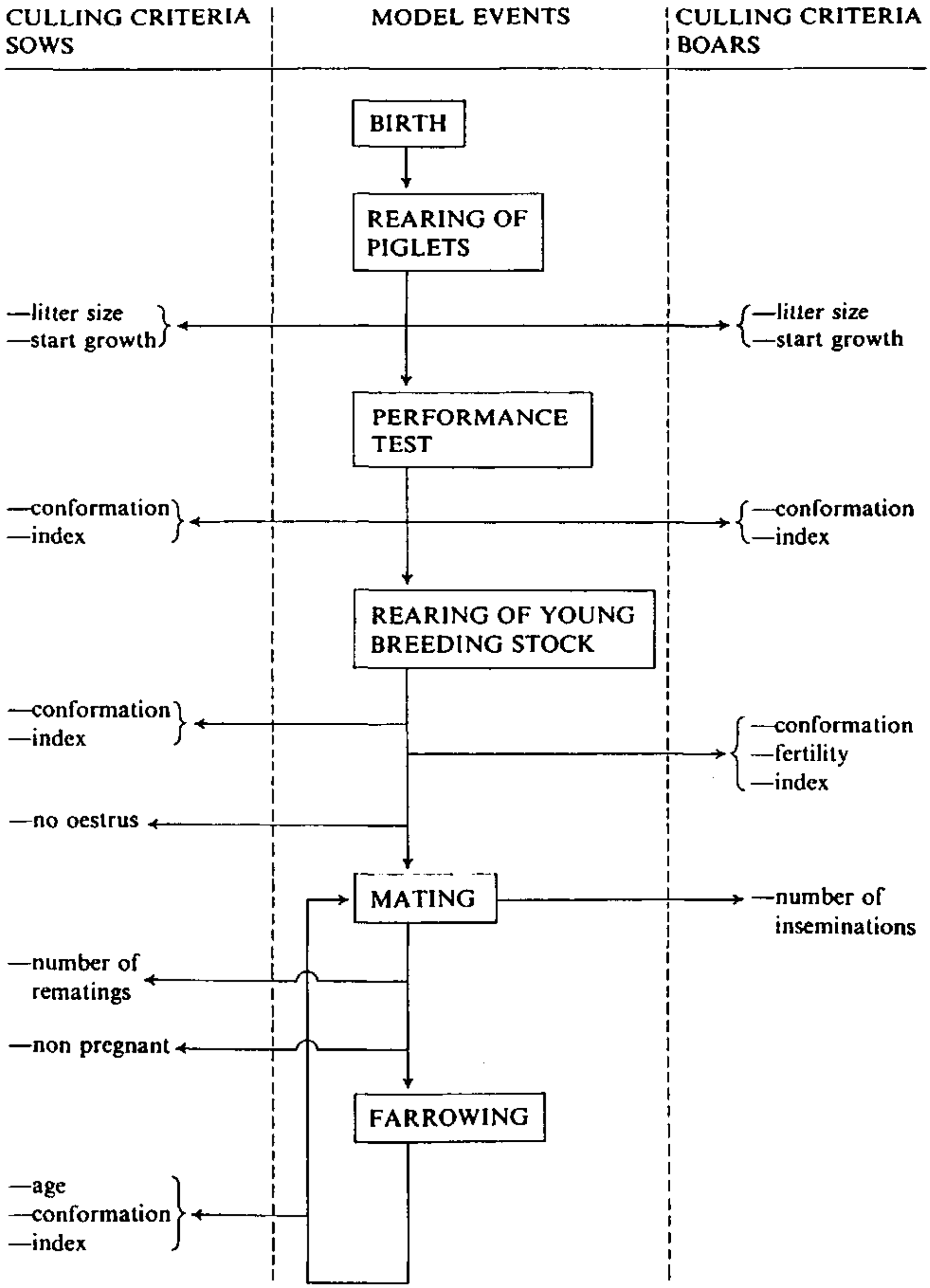

Fig. 2. Life cycle of animals in a pig nucleus situation and reasons for culling.

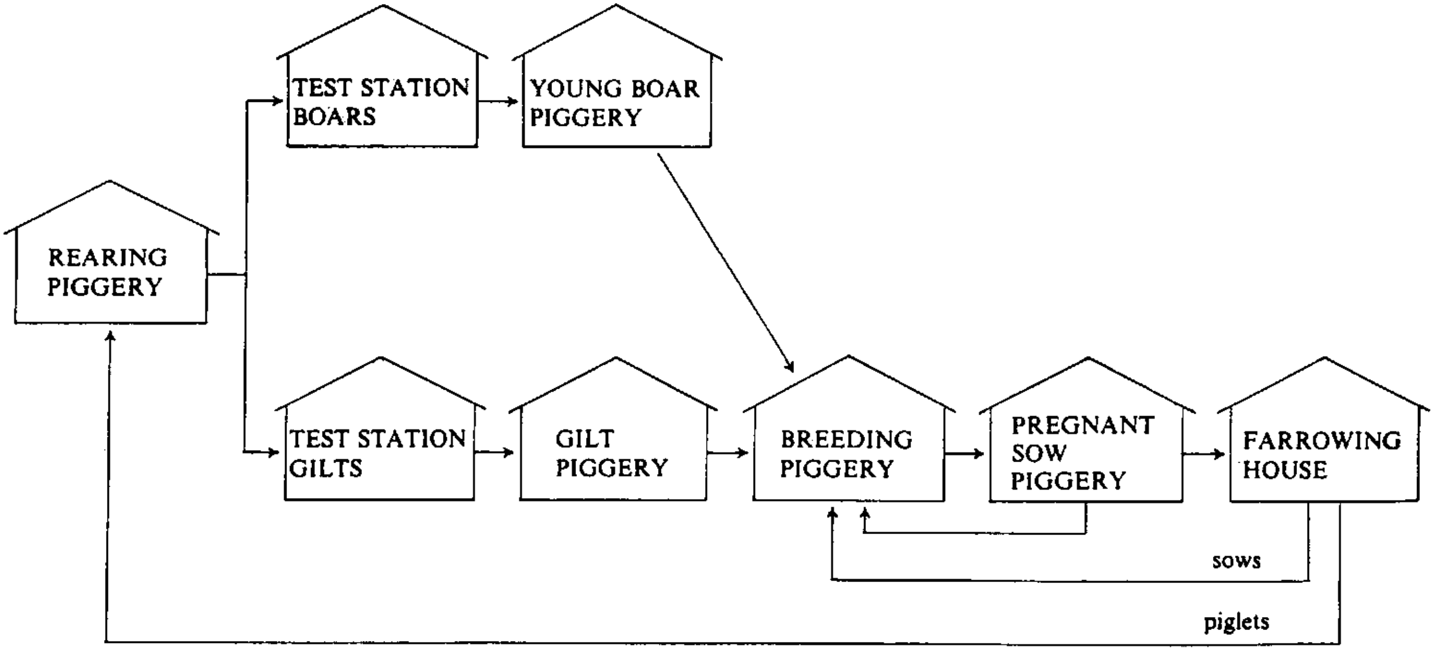

Fig. 3. Pig houses distinguished by the model. The arrows indicate the flow of animals from one pig house to the other.

Table 1. Traits in the model.

Trait	True breeding value (both sexes)	Phenotypic value	
		sows	boars
Growth rate 0 to 23 kg	+	+	+
Growth rate 23 to 100 kg	+	+	+
Feed intake	+		+
Estimated lean percentage	+		+
Side fat thickness	+	+	
Age at first oestrus	+	+	
Litter size at birth	+	+	
Interval weaning-oestrus		+	

be explained by this estimator (Kanis et al., 1986). Lister (1984) signals a promising development of equipment to estimate lean percentage in live animals. Data of Kempster et al. (1982), Busk (1985) and Molenaar (1985) suggest that an R^2 of 0.70 is attainable. Such a method might be too costly to be applied to sows because the possible selection intensity is lower than in boars. The model assumes a testing system that enables recording of growth rate from 23 to 100 kg, individual feed intake and estimated lean percentage (R^2= 0.70) for boars and of growth rate and side-fat thickness for sows. Meat quality is not included in the model because this trait is not yet clearly defined.

Litter size at birth, piglet mortality, interval weaning-oestrus and age at first oestrus are vital reproduction traits (Legault et al., 1975; Knap, 1985). Litter size at first and later parities should be considered as different traits (Knap, 1985; Vangen, 1986), however, a genetic correlation of unity is assumed in the model. Husbandry plays a major role in piglet mortality (Legault et al., 1975). For this reason, a true breeding value is generated for litter size at birth instead of litter size at weaning. Maternal effects are ignored.

The distribution of the interval weaning-oestrus deviates from normality (Aumaître et al., 1976; Fahmy et al., 1979; Merks et al., 1986). Data presented by Merks et al. (1986) suggest a multiple peak distribution. A physiological reason for this phenomenon could be the occurrence of silent heat, the major reason for a prolonged weaning-oestrus interval according to Benjaminsen and Karlberg (1980). A multiple exponential distribution with two characterizing parameters (Koops, 1986) appears to fit acceptably to the data of Merks et al. (1986). From the breeding point of view, number of sows that show heat in the first oestrus cycle (P_{heat1}) is the most important parameter. Mean interval weaning-oestrus within respective oestrus cycles is the second parameter.

Genetic parameters of P_{heat1} are unknown; thus the trait is only considered at the phenotypic level. Random deviates from a uniform distribution are used to simulate P_{heat1}. If the assigned value exceeds a threshold, the animal will not show heat within three weeks. This threshold is dependent on parity (Radev et al., 1976; Pepper and Taylor, 1977; Karlberg, 1980). P_{heat1} can vary considerably between lines (N.P.B.O. and I.V.O., 1981) and is a variable in the model.

It is assumed that an exponential distribution (Gilchrist, 1984) can describe the cumulative probability distribution of the interval weaning-oestrus (IWO) within the first oestrus cycle.

$$\text{Cumprob} = 1 - \exp((\text{IWO}-\text{IWO}_{zero})/(\text{IWO}_{mean}-\text{IWO}_{zero})) \qquad (1)$$

where IWO_{zero} : minimum length of IWO minus one day,

IWO_{mean} : mean length of IWO.

IWO_{zero} is assumed to be three days for physiological reasons (Cole and Cupps, 1977). IWO_{mean} is dependent on parity (table 2).

Age at first ovulation in gilts is assumed to be normally distributed. A number of gilts will not show heat within three weeks after transfer to the breeding piggery. This event is simulated similar to P_{heat1} in sows.

No true breeding value is generated for conformation because genetic important traits have not been identified yet.

2.3 Basic parameters

The program starts with a module called PARAM, which assigns a value to basic parameters in the model, for example, number of founder boars and sows, desired size of the nucleus population, allowed degree of relationship between mates, maximum number of parities per sow, test capacity and maximum number of boars and gilts tested per litter.

Table 2. Parity-dependent traits: mean levels for litter size at birth (LSB) and interval weaning-oestrus (IWO), probabilities of culling sows for insufficient conformation or health problems (PC)[a] and correction factors for piglet survival (CPS).

Parity	LSB	IWO	PC	CPS
1	9.8	9.9	10.0	1.000
2	10.6	7.2	7.0	1.034
3	11.4	6.3	7.5	1.034
4	11.9	6.0	10.0	1.034
5	11.9			1.034

[a] expressed as a percentage of total number of farrowing sows in the same parity group.

2.4 Foundation of the population

Subroutines FOUNDERSOW and FOUNDERBOAR produce the founder population. A phenotypic value for each trait of animal i is computed as

$$P_i = B + A_i + E_i \tag{2}$$

where P_i : phenotypic value,
B : base level,
A_i : true breeding value,
E_i : random environmental component.

IMSL routine GGNSM (IMSL, 1984) is used to generate a correlated set of true breeding values and a set of correlated random environmental components for each animal. The technique used is described by Brascamp (1978).

Base levels and other phenotypic and genetic characteristics of traits in the model are presented in tables 2 - 4. Parameters are chosen to represent a Dutch sire line (Merks, 1983, 1984; Van der Steen, 1984; Knap, 1985; Knap et al., 1985; Kanis, 1986; Knap, 1986; Van der Steen et al., 1986; Walstra, 1986).

Mean levels and standard deviations for production traits of sows and boars differ because of an assumed difference in feeding regimen: boars are

Table 3. Mean levels, heritabilities (h^2) and phenotypic standard deviations (σ_p) for traits in the model.

Trait	Mean	h^2	σ_p
boars			
growth rate 0 to 23 kg ($g.d^{-1}$)	350	0.10	37
growth rate 23 to 100 kg ($g.d^{-1}$)	900	0.25	88
feed intake ($g.d^{-1}$)	2 400	0.25	200
estimated lean percentage	52	0.45	2.5
side fat thickness (mm)	[a]	0.30	1.15
sows			
growth rate 0 to 23 kg ($g.d^{-1}$)	350	0.10	37
growth rate 23 to 100 kg ($g.d^{-1}$)	785	0.20	42
side fat thickness (mm)	12.2	0.30	0.90
age at first oestrus (d)	240	0.12	10
litter size at birth	[b]	0.10	2.84

[a] not used in the model.

[b] dependent on parity (table 2).

Table 4. Genetic (above diagonal) and phenotypic correlations for production traits in the model.

	GR	FI	LEAN	SF
growth rate 23 to 100 kg (GR)	--	0.85	-0.15	0.00
feed intake (FI)	0.65	--	-0.35	0.40
estimated lean percentage (LEAN)	-0.10	-0.30	--	-0.40
side fat thickness (SF)	0.10	[a]	[a]	--

[a] Not used in the model.

fed ad libitum, whereas sows are kept on a restricted diet. Feeding level has a phenotypic effect only. Genetic correlation between similar traits on different diets is assumed to be unity.

Genetic parameters concerning estimated lean percentage (LEAN) are lacking. Parameters from Knap et al. (1985) concerning ham and cutlet percentage are adapted with the assumption that R^2 of the estimation equals 0.70.

An animal needs a certain minimum amount of lean, fat and bone to survive. For this reason, minimum and maximum levels for LEAN are assumed to be 35 and 75 percent, respectively. Choice of bounds implies that response to selection will diminish at the approach of the bounds. A reversed logistic transformation (Gilchrist, 1984) is used for this purpose. A phenotypic value for LEAN is obtained in four steps (figure 4). The value on a normal scale, generated by (2), is first transformed to a logistic scale:

$$\mathrm{LEAN}_{lg} = \mathrm{LEAN}_{lgm} + (\mathrm{LEAN}_{n} - \mathrm{LEAN}_{nm}) * \sigma_{lg} / \sigma_{n} \qquad (3)$$

Mean and standard deviation on the normal scale are assumed equal to mean and standard deviation on the observed scale at the foundation of the population. This is reasonable because the mean on the binomial scale is not far from fifty percent.

LEAN is a binomially expressed trait; a value on a binomial scale is obtained from

$$\mathrm{LEAN}_{bin} = \exp(\mathrm{LEAN}_{lg}) / \; (1 + \exp(\mathrm{LEAN}_{lg}) \qquad (4)$$

	scale	*mean*	*σ*
(1) LEAN_n ↓	normal	LEAN_{nm}	σ_n
(2) LEAN_{lg} ↓	logistic	LEAN_{lgm}	σ_{lg}
(3) LEAN_{bin} ↓	binomial (0–1)	—*	—*
(4) LEAN_{obs}	observed binomial (35–75%)	LEAN_{obsm}	σ_{obs}

* Not used in model equations.

Fig. 4. Generation of a phenotypic value for estimated lean percentage (*LEAN*).

Finally, rescaling keeps lean percentage within reasonable bounds:

$$LEAN_{obs} = 35 + 40 * LEAN_{bin} / 2.5 \tag{5}$$

$LEAN_{lgm}$ and σ_{lg} can be obtained from a reversed application of (5) and (4) with $LEAN_{obs}$ equal to $LEAN_{obsm}$ and $LEAN_{obsm} + \sigma_{obs}$, respectively.

Production traits are assumed not correlated with reproduction traits (Legault, 1971; Morris, 1975; Young et al. 1978; Johansson, 1981; Bereskin, 1984; Brien, 1986). Correlations between reproduction traits in the model are also assumed to be zero.

Equation (2) is applied assuming no genotype - environment interaction. This is not unreasonable because the model deals with a nucleus situation with a standardized feeding and housing system.

Founder animals are assumed to have no production records. Thus, the best estimate of their breeding value for production traits is zero. Founder boars start their reproductive life 8 months of age. Mean age at sexual maturity is 240 days for sows (table 3). Founder sows enter the breeding herd at 240 days plus 0, 1 or 2 weeks, with a percentage probability of 50, 30 or 20.

2.5 Selection of sows

Subroutine SEL_SOW determines which sows enter the breeding piggery. Number of sows to be selected depends on size of the nucleus population. The aim is to use available pig houses efficiently throughout the year. This applies especially to the farrowing house with its relatively expensive equipment. Therefore, it is desired to have a constant number of sows enter the breeding piggery in a period of W weeks, where W is length of time a sow occupies a place in the farrowing house. W comprises adaptation period (1 week), suckling period (5.5 weeks) and a cleaning period (0.5 week). Length of the suckling period is not integer because weaning takes place weekly.

Desired number of sows in W weeks (DNS_{tot}) is

$$DNS_{tot} = NRSOWS * FARROWINDEX * C * W / 52 \tag{6}$$

where NRSOWS : size of nucleus sow population, defined as total number of sows in breeding, gestation and farrowing houses,

FARROWINDEX : expected average number of farrowings per sow per year,

C : correction factor.

The product of the first two terms in (6) equals expected number of farrowings per year. Number of sows that should yearly enter the breeding piggery can be obtained by multiplying by C. This correction factor accounts for number of sows failing to produce a litter.

From DNS_{tot} and actual number of sows that entered the breeding piggery in the last W-1 weeks, a desired number of sows to be selected in week t can be computed:

$$DNS_t = DNS_{tot} - \Sigma_{i=t-W+1}^{i=t-1} NS_i \tag{7}$$

where NS_i : actual number of sows that entered the breeding piggery in week i.

NS_i is dependent on number of sows available for selection. Due to random fluctuations in number of weaned sows and number of sexually mature gilts, NS_t can be too small to meet DNS_t. This shortage can be complemented in the next weeks as seen from (7). However, to prevent too large fluctuations in number of new sows (and thus in selection intensity) an upper and a lower bound are set to DNS_t:

$$MAXDNS = 1.5 * DNS_{tot} / W \tag{8}$$

$$MINDNS = 0.5 * DNS_{tot} / W \tag{9}$$

Selection of best sows and gilts is based on an index that combines production and reproduction traits included in the model (table 1). Prior to this index selection, weaned sows are subject to two other culling criteria, independent of the sow's performance for (re)production traits. Firstly, parity number of the sow is compared to maximum number of parities allowed. Secondly, sows can be culled for insufficient conformation or health problems. The probability of being culled, expressed as a percentage of number of farrowing sows in the same parity group, is in table 2. The relative culling probability per parity is based on data from Bisperink (1979), Buiting and Merks (1986) and Van Steenbergen (1986). These data concern the multiplier level in the production pyramid. Culling at the nucleus level is assumed about twice as high because of a higher selection pressure on conformation.

Gilts have to compete with weaned sows for a place in the breeding piggery. They enter this competition when they are 240 days and have an opportunity of being selected during a period of three weeks. At weaning, sows get only one opportunity of being selected.

2.6 Sowcycle

Three different pig houses are distinguished for sows: a breeding piggery, a piggery for pregnant sows and a farrowing house. For gilts that enter the breeding piggery, a mating date is calculated from their birth date and age at first oestrus. Gilts who already were in oestrus before entering get an appropriate date by adding a multiple of 21 days to date of first oestrus. Mating date of sows is determined by weaning date and length of interval weaning-oestrus (IWO). Rearrangement of (1) leads to

$$IWO= IWO_{zero} - (IWO_{mean}-IWO_{zero}) * \ln(1-Cumprob) \qquad (10)$$

Phenotypic values for IWO are obtained from (10) by replacing (1-Cumprob) by a random deviate from a uniform distribution. Sows not showing heat within three weeks are culled.

After mating, sows are transferred to the pregnant sow piggery. A random number is assigned to each sow to decide whether it is going to bring a litter or not. The farrowing probabilities for first, second and third to fifth parity are 82, 81 and 84 percent (Bisperink, 1979). When the sow is not going to farrow, another random number is assigned to the animal and it is classed into one of the following categories :

(1) oestrus day 21 (regular oestrus, 35 %)
(2) oestrus day 24 - day 35 (irregular oestrus, 9 %)
(3) oestrus day 40 (31 %)
(4) oestrus or abortion day 41 - day 107 (14 %)
(5) no oestrus or mummification of embryo's (11 %).

The probability distribution is based on a literature review by Arts (1981).

For animals in categories (2) and (4), an equal distribution of the probability of occurrence of the respective event over the time period is assumed. Percentage probability for category (3) is the sum of probabilities that sows show heat spontaneously in the sixth week after first mating and that sows show heat after a negative pregnancy diagnosis followed by oestrus induction. Sows in category (5) are not identified as such until their expected farrowing date. Sows from the categories (4) and (5) are culled.

Each week, all sows in the pregnant sow piggery are checked for occurrence of one of the events mentioned above. Sows thought to be pregnant are transferred to the farrowing house one week before expected farrowing. Number of rematings of sows from categories (1), (2) and (3) is checked. When maximum is not exceeded, remating is performed and the process of assigning one of the possible events to the sow is repeated. When maximum is exceeded the sow is culled. Farrowing probabilities for first and second rematings are 66 and 53 % (Bisperink, 1979), irrespective of parity number.

Pregnant sows farrow during their second week in the farrowing house. Subroutine BIRTH, which assigns characteristics to the litter born, is described in a subsequent section. Weaning takes place weekly, so age of litters at weaning can differ by as many as 6 days.

2.7 Boar management and mating

Size of the nucleus boar population, e.g. total number of boars in service every year, and number of boars to be present at the same time must be specified. From the point of view of costs, the latter number should be small. The intention to avoid mating of relatives, however, requires a sufficient number of boars to be present. Annual number of boars used and number of boars present at the same time are variables in the model.

As a rule, every boar performs a specified number of inseminations and is culled afterwards. This number is computed according to:

$$\text{NRINSEM} = \text{FARROWINDEX} * \text{INSEMFARROW} * \text{NRSOWS} / \text{NRBOARS} \qquad (11)$$

where INSEMFARROW : average number of inseminations needed for one farrow,

NRBOARS : size of nucleus boar population.

An exception to this rule is made when there is no young boar available for replacement. In this case, the boar stays until replacement is possible. As a result, turn-over of boars per year can deviate slightly from the number specified in PARAM.

Boars mate sequentially. This insures that inseminations of a boar are done within a reasonable time period. However, the genetic relationship of sow and boar is checked before mating. Subroutine CALC_FVALUE is used for this purpose. The algorithm takes account of all pedigree information since foundation of the population. The allowed degree of relationship is a variable in the model.

2.8 Generation of offspring

Subroutine BIRTH is called for every litter born. Compared to litter size at birth, litter size at weaning is reduced by stillbirth and by death during the suckling period. Random culling is performed to model these events. Analysis of a set of field data, that contained more than 14 000 litter records, showed that the probability that a piglet survives up to weaning depends on litter size at birth and on parity number of the sow (Van der Steen et al., 1986). Survival probabilities and parity correction factors are in tables 2 and 5. Sex ratio in the litter is determined by chance (expected ratio 1 : 1). Number of boars from each litter that should be tested can be varied. As many gilts as possible are tested up to a maximum of six gilts per litter.

Table 5. Percentage probability that piglets survive up to weaning (PSW) in dependance of litter size at birth (LSB) for first parity sows.

LSB	1	2	3	4	5	6	7	8	9	10
PSW	38	68	76	82	82	85	85	85	85	83

LSB	11	12	13	14	15	16	17	18	19	20
PSW	81	79	76	72	69	65	61	57	54	52

Correlated random numbers are generated to calculate breeding values and phenotypic values as in section 2.4. Breeding values are calculated as

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{}(0.5 * CF) * a * \sigma_A \qquad (12)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \qquad (13)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,
CF : correction factor that accounts for the reduction in additive genetic variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),
a : random normal deviate,
σ_A : additive genetic standard deviation.

A phenotypic value is calculated as an extension of (2):

$$P_i = B + A_i + E_i - bF * F_i \qquad (14)$$

where bF : regression coefficient that reflects the degree of inbreeding depression,
F_i : inbreeding coefficient of individual i.

Inbreeding depression is expected for traits subject to dominance as, for example, fertility traits (Falconer, 1981). The degree of inbreeding depression is a variable in the model and is trait-dependent.

After weaning, piglets are transferred to a rearing pen where they stay until they weigh 23 kg. Within-litter selection of animals to be tested is performed at that time. This selection is done at random, with the restriction that a minimum start growth (growth up to 23 kg) is required. This minimum level can be varied.

2.10 Performance testing for production traits

2.10.1 Use of available test capacity

The test station consists of several divisions. To make application of an all in-all out system possible, differences in weight at start of test should not be too large. Size of divisions is chosen in such a way that, on average, two weeks are needed to fill a division with new piglets. Begin and end of test are determined by weekly weighings. Piglets enter the test station at the end of the week in which they reach a weight of 23 kg. They leave the test station as soon as they reach 96 kg.

The line that is studied is assumed to be one of the lines of a breeding company. This means that representatives of several lines will be present in the same division. In the practical situation, number of test places occupied by different lines will resemble the fluctuating number of piglets to be tested. Management of other lines, however, lies outside the scope of the model. For this reason, a maximum number of test places to be occupied by the line under study (TP_{max}) must be chosen. It is assumed that this maximum exceeds the average test capacity used by the line by EXTRA places: EXTRA equals three and five for boars and sows, respectively. The average number of test places occupied depends on size of the line and number of animals tested in every litter. Thus,

$$TP_{max} = 2 * ATL * NRSOWS * FARROWINDEX/ 52 + EXTRA \qquad (15)$$

where ATL : average number of gilts or boars tested per litter.

Because of fluctuations in number of farrowings and in litter size, number of piglets to be tested will occasionally exceed available test capacity. In this case, the excess number of piglets is not tested. Culling is based on start weight. It is assumed that every two weeks a new division is opened. This means that actual number of test places used by the line under study can vary from zero to TP_{max}.

As many animals as possible should complete the test. Preliminary culling biases estimation of a contemporary average (CA) for a batch of test pigs and, thus, calculation of selection indices. From a practical point of view, however, a poor grower can not endlessly stay on test, for two reasons. Firstly, the number of divisions is limited, which means that after a number of weeks the presently used division should be emptied to make room for new test pigs. Secondly, test results will be less reliable when number of animals in the division becomes small. It is more difficult to keep climatic conditions constant in that situation. With the assumption that mean and standard deviation of growth rate for all lines on test are 850 88 g.day^{-1} for boars and 700 42 g.day^{-1} for sows, a probability distribution for number of weeks needed to complete the test can be calculated (table 6). Based on these figures, the choice is made to empty a division of test boars 15 weeks after the first boar entered the division. For sows, the maximum number of test weeks is chosen to be 17. Test results from non-

Table 6. Cumulative percentage of animals that completed the performance test as a function of number of weeks on test.

weeks on test	10	11	12	13	14	15	16	17
boars that completed testing	1	13	41	71	88	96	99	
sows that completed testing				1	14	55	87	98

finishers can be estimated from obtained records and are incorporated into the calculation of contemporary averages. A couple of days are needed to clean a division. As a result, a batch of boars and sows keeps a division occupied for 16 and 18 weeks, respectively. This means that 9 divisions are needed in the gilt test station and 8 in the boar test station.

2.10.2 Selection

Final test weight corresponds to market slaughter weight. Therefore it is important to decide immediately whether the animal has to be culled. For this reason, as a first step of selection a preliminary index is calculated using the most recent calculated contemporary average. This index should be above a minimum to prevent the animal from being slaughtered. This minimum is a variable in the model.

When the division is emptied, an average for all traits for the present batch is calculated. This mean is used as a contemporary average in calculation of indices. Data of animals from other lines are incorporated in this calculation. A mean index for other lines is generated by means of a random deviate from a normal distribution. Mean of this distribution is equal to mean of the last six batches. The standard deviation equals the standard deviation of an index based on data from a single individual divided by the square root of the actual number of animals from other lines in the batch. Total number of test places in a division is chosen to be 50. Test capacity is assumed to be fully used.

New indices are calculated as soon as CA is known. Animals that do not meet minimum requirements of index and conformation are culled. Scoring for conformation is based on a random number assigned to every animal; the probability that an animal is culled because of insufficient conformation is a variable.

2.11 Selection and management of young breeding stock

It is assumed that conformation of gilts is judged again at mean age of sexual maturity. Culling probability is a variable. The selection process which starts thereafter is already described in section 2.5.

A number of boars will not reach sexual maturity because of a reduced performance for production traits or because of conformation problems. The remaining boars are tested for reproductive performance (mating behavior, sperm quality and quantity). These events are modelled by random culling of a number of animals. Culling probability is also a variable in the model.

Next step of selection is the decision whether a young boar is good enough to enter the young boar pool, which is a limited number of young boars from which new breeding boars are selected. Selection is based on index of the boar. Size of the pool is a variable in the model. The limited size means that there is continuous selection. A pool member with a relatively low index will be culled as soon as a boar with a higher index is available. Boars that are not selected for breeding within 8 weeks are culled with an exception for those with an index of one standard deviation above mean index; their maximum stay is 12 weeks.

3. EXAMPLE

3.1 Parameters

As an illustration, the model is applied to a sire line with characteristics as in table 7. Number of founder sows applies to number of sows that is expected to bring at least one litter. P_{heat1} is assumed to be 70, 70, 80 and 85 percent for gilts and for first, second and later parity sows, respectively. With an expected farrowing index of 2.2 and a correction factor (C) of 1.4, DNS_{tot} equals 21 sows in 7 weeks. C is based on the expectation that 70 percent of sows that enter the breeding piggery will farrow. The expected value of INSEMFARROW is 1.25, which leads to nine inseminations per

Table 7. Characteristics of the line in the example.

General	
number of sows	50
number of boars	15
number of founder sows	50
number of founder boars	15
number of young boars	3
number of breeding boars	3
Test	
number of boars tested per litter	2
minimum start growth ($g.d^{-1}$)	300
minimum litter size at weaning	6
minimum index at end of test, boars	100
minimum index at end of test, sows	68
percentage of boars culled for conformation	40
percentage of gilts culled for conformation	20
Sexual maturity	
percentage of boars culled for reproduction or conformation	40
percentage of gilts culled for conformation	20

breeding boar (eq. 11). Breeding goal (H) and index (I) only include production traits and are defined as

$$H = 0.178 * A_{GR} - 0.05 * A_{FI} + 3.0 * A_{LEAN} \tag{16}$$

$$I_{boars} = 0.0212 * P_{GR} - 0.0004 * P_{FI} + 1.5548 * P_{LEAN} \tag{17}$$

$$I_{gilts} = 0.0357 * P_{GR} - 2.5965 * P_{SF} \tag{18}$$

where A_i,P_i: breeding values and phenotypes for trait i,
GR : growth rate 23 to 100 kg ($g.day^{-1}$),
FI : feed intake ($g.d^{-1}$),
SF : side-fat thickness (mm).

Economic values in H are chosen according to Noordam et al. (1986) and index weighing factors are obtained using selection index procedures (Hazel, 1943). Only own performance data are included in the index. Index values are standardized at a mean level of 100 with a standard deviation of 32.

The model covers a period of 25 years. Results are presented as means of 10 replicate runs.

3.2 Results

Despite relatively low farrowing indices, number of sows stabilizes at a value close to 50 as desired (table 8). The expected value of 2.2 was too optimistic because of the relatively long suckling period and a high incidence of anoestrus. Underestimation of the factor C, due to an unexpected high proportion of gilts in the herd, compensates for the overestimation of the farrowing index in the calculation of DNS_{tot}.

Gilts that have finished test but are not yet involved in breeding consist of sexually mature and immature gilts. The former group includes about 40 gilts, which means that 5 gilts mature each week on average. This offers good selection possibilities: about 50 percent of culled sows and gilts are culled because of a low index (table 9). Anoestrus is a major problem in

Table 8. Number of sows and time-course of their reproductive performance.

Year	Number of sows	Farrowing index	Number of inseminations per farrowing	litter size at birth	litter size at weaning
1	30.0	1.64	1.83	9.77	7.79
2	41.9	1.86	1.54	10.31	8.22
3	47.5	2.08	1.27	10.40	8.34
4	48.8	2.11	1.25	10.45	8.32
5	50.3	2.06	1.28	10.30	8.20
6-10	49.7	2.10	1.26	10.41	8.30
11-15	49.7	2.11	1.27	10.63	8.38
16-20	49.5	2.10	1.26	10.70	8.47
21-25	50.2	2.11	1.26	10.78	8.50

Table 9. Percent distribution of number of culled sows per reason for culling.

Reason for culling	Gilts[a]	Sows[b]
failure to breed after repeated mating	0.6	0.9
barren	1.1	1.8
no oestrus	19.1	24.8
abortion or late oestrus	1.5	2.3
age	0.0	5.4
leg problems	25.9	14.8
index	51.8	50.0
Total number culled per year	175	60

[a] end of test to first parity

[b] first to fifth parity

both gilts and sows because of the relatively low values chosen for P_{heatl}. The importance of leg problems as a reason for culling is as expected.

About 60 percent of farrowings are by first parity sows (table 10). This high proportion would be even higher if corrections for genetic trend were incorporated in selection of sows. The important contribution of gilts is partly due to the selection policy followed at weaning; no more than DNS_t sows can be selected for breeding. The high sow turn-over also reflects a breeding goal for production traits only; a reliable estimation of breeding values is possible at an early age and enables a short generation interval.

Despite selection pressure on production traits, litter size at birth shows a slight increase (table 8). This is due to mild selection on litter size at start of the performance test and to the higher probability for gilts from larger litters of being selected because number of tested gilts per litter increases with litter size. The increase of litter size is questionable because improvement of this trait is considered to be difficult (Bichard and David, 1985; Legault, 1985). Compared to theoretical expectations of selection response for litter size (Bichard and David, 1985; Legault, 1985; Avalos and Smith, 1987), however, the increase of litter size in the model is negligible.

Table 10. Percent distribution of farrowings per parity and per year.

Year	Parity				
	1	2	3	4	5
1	90.3	9.7	0.0	0.0	0.0
2	53.8	29.1	13.7	3.4	0.0
3	59.2	25.8	8.8	4.4	1.8
4	61.5	20.8	10.4	4.9	2.3
5	60.6	22.1	8.5	5.3	3.6
6-10	59.6	20.6	9.9	6.0	3.8
11-15	59.7	20.2	10.2	6.3	3.6
16-20	61.4	20.5	9.9	4.9	3.3
21-25	58.8	20.5	10.4	6.5	3.8

Number of inseminations per farrowing does not deviate from expectation. Number of boars used per year is somewhat lower than desired (table 11), because of a low boar turn-over in the first couple of years and the relatively severe selection in young boars. This can lead to a temporary shortage of replacement boars. As an extreme, one boar performed 26 inseminations in 28 weeks; however, average number of inseminations per boar is close to the desired value.

The high maximum value of the inbreeding coefficient (F) in boars illustrates that the level of this trait is not incorporated in the selection process. From year three onward the average level of F in performance-tested gilts increases linearly up to 17.9 percent after 25 years. The rela-

Table 11. Some characteristics of breeding boars.

	Mean	Min	Max
number of boars per year	14.2	9	17
number of matings per boar	9.1	9	26
inbreeding coefficient (%)	9.3	0	43.6
index	132	100	203
number of weeks in service	11	6	28

tive annual increase of ΔF, ΔF (Falconer, 1981), is 0.8 percent, which corresponds to an effective population size of 64. As a result of the breeding scheme ΔF is higher than the 0.6 percent that follows from the well known formula of Wright (1931). Variance in number of offspring per parent in the model will be higher than assumed by Wright (1931).

Results of selection on the time-course of production traits are in figures 5 and 6. Age distribution of animals is stable from year five onward. Annual response for breeding goal traits GR, FI and LEAN is 5.8 $g.d^{-1}$, -0.2 $g.d^{-1}$ and 0.42 percent, respectively. To validate the model, expected response should be calculated. Expected selection intensities can only be estimated roughly; taking account of involuntary disposal, a selection of 1 of 5 in boars seems a reasonable approximation. This leads to a selection

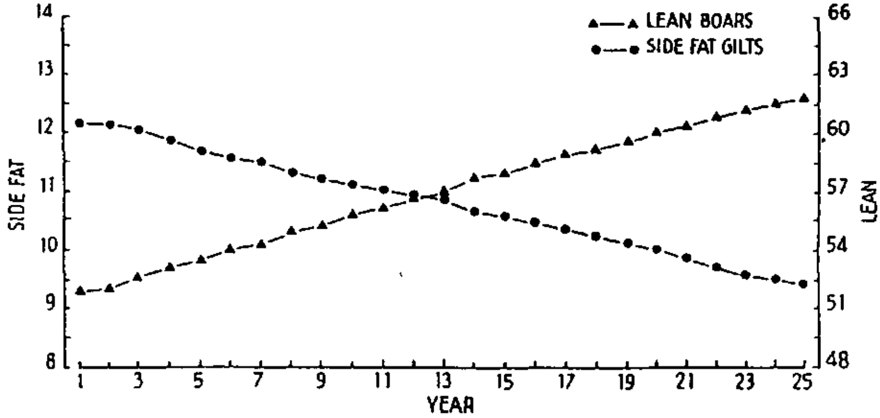

Fig. 5. Course over time of estimated lean percentage (*LEAN*) in boars and side fat thickness (mm) in gilts.

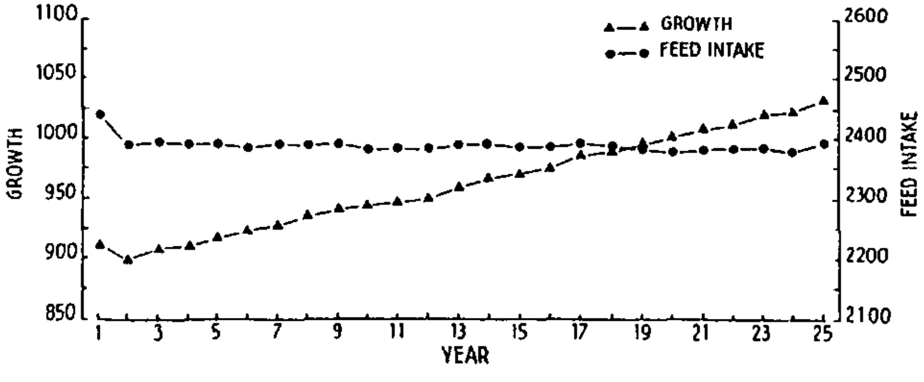

Fig. 6. Course over time of growth (g day^{-1}) and feed intake (g day^{-1}) in boars.

intensity of about 1.2 (Becker, 1975). In gilts, with a weekly selection process, the number selected will vary between 3 from 5 to 1 from 3. Selection intensity will be around 0.6. The contribution of selection in sows to selection response can be assumed equal to the contribution in gilts because the higher selection intensity is compensated for by a prolonged generation interval. Expected response for GR, FI and LEAN is 6.6 $g.d^{-1}$, -1.7 $g.d^{-1}$ and 0.68 percent, respectively. For GR and FI, this agrees with realized values, despite that selection intensities are overestimated. Response for LEAN decreases over time as realized values approach the biological maximum. As a result, realized response is smaller than expected from selection index theory.

Results show that the model can be used to study breeding schemes in a small pig population. It offers opportunity to make further investigations on effects of population size and structure, size of founder population and different selection and mating systems on selection response and inbreeding coefficient.

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Chapter 3

STUDIES ON BREEDING SCHEMES IN A CLOSED PIG POPULATION

1. Population size and selection intensities

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ABSTRACT

A stochastic model was used to examine effects of variation in population size on selection response and inbreeding coefficient in a closed swine herd. An additive genetic model was followed, each trait was assumed to be affected by many unlinked loci of small effect each. Selection was on traits applicable to a sire line. Results were compared to expectations from selection index theory and from theory of effective population size.

Advantages of intense selection in short-term response were less than expected because of reduced genetic variance from linkage disequilibrium and reduced selection intensity from small numbers of families. Comparison of alternative breeding schemes should include corrections for these effects.

Response was curvilinear with time, and curvilinearity increased with intensity of selection. Increased relationships between animals caused reduced variance available for selection and diminished response. When the time period included in the evaluation of breeding schemes increased, optimal annual number of boars also increased.

Equations were derived to describe cumulative response in year 25 as a function of size of the sow herd and annual number of boars. With 25, 50, 100 and 150 sows, 52, 66, 75 and 84 percent of maximum response with an infinite number of sows was attained. Optimal annual number of boars depended on size of the sow herd: when herd size increased, optimal annual number of boars increased to 15.

Drift caused considerable differences in response between replicates. These differences, however, were small compared to differences in means between sow alternatives. Splitting of a line into independent sublines, therefore, is unadvisable, because of reduced expected response due to smaller population size.

1. INTRODUCTION

Population size at the nucleus level is important with respect to costs and benefits of pig breeding. Selection response is dependent on number of boars and of sows available for selection and on number of each sex used for breeding. Knowledge of influence of population size and selection intensity on progress of production and reproduction traits and inbreeding coefficient over time is limited.

In closed finite populations, drift and selection each has an effect on the mean and genetic variance for different traits. Drift causes random loss of alleles and reduces genetic variation available for selection. Assuming infinite time, Robertson (1960) stated that 50 percent of the population should be selected for breeding. The time period of interest to animal breeders, however, is limited to 10 or 20 generations. Work of Smith (1969, 1981), Robertson (1970a) and James (1972) showed that more intense selection is optimal in this situation. Optimal selection intensities for mid-term response to selection, however, are lower than expected from short-term theory (Smith, 1969).

Selection policy influences effective population size and hence the amount of drift. Selection also invokes linkage disequilibrium (Bulmer, 1971; Robertson, 1977) and reduces genetic variance available for further selection (Bulmer, 1976; Fimland, 1979; Mueller and James, 1983a,b; Sörensen and Hill, 1983; Sörensen and Kennedy, 1983).

Pig nucleus breeding involves overlapping generations and continuous farrowing and selection. Optimal selection intensities for such a breeding scheme are not easily derived (James, 1972; Smith, 1981). De Roo (1987) described a stochastic model that examined breeding schemes in a closed pig population. This model is used here to study effects of population size on selection response and inbreeding coefficient. Results are compared to expected values of selection response and inbreeding coefficient by means of selection index theory and of theory of effective population size (Wright, 1931).

2. MATERIAL AND METHODS

2.1 Model

The model described by De Roo (1987), measured changes in production and reproduction traits and inbreeding coefficient over 25 years of selection in a closed swine herd. Growth rate (23 to 100 kg), feed intake, lean percentage, litter size and interval from weaning to oestrus were incorporated in the model because of their economic relevance to pig breeders. The model included overlapping generations, continuous mating and farrowing and weekly selection of boars and sows. Week was the unit of time.

As long as the genetic mechanism of the inheritance of traits is not fully known, assumptions about the genetic model need to be made. De Roo

(1988) argued that an infinitesimal model, in which traits are affected by an infinite number of unlinked loci of small effect each, would provide useful information to pig breeding. An additive, infinitesimal model was used in this paper, epistatic effects were ignored. Breeding values were generated as

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{(0.5 * CF)} * a * \sigma_A \quad (1)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \quad (2)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,
CF : correction factor that accounts for the expected reduction in additive variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),
a : random normal deviate,
σ_A : additive genetic standard deviation.

Besides the effect of inbreeding on the additive genetic variance, it is also expected to have an effect on the mean of traits subject to dominance (Falconer, 1981). The impact of both effects on response needs to be investigated. To prevent confounding of these inbreeding effects, inbreeding depression was ignored in the present paper.

Phenotypes were simulated as

$$P_i = B + A_i + e * \sigma_E \quad (3)$$

where P_i : phenotypic value,
B : base level,
e : random normal deviate,
σ_E : environmental standard deviation.

Based on previous results, the way in which litter size at birth was determined by De Roo (1987) was changed, and ovulation rate and prenatal survival were introduced as components of litter size (appendix).

A second adaptation of the model concerns management of breeding boars. Boars were assumed to perform a fixed number of inseminations. This does not, however, insure a regular selection of new boars and occasionally a group of boars must be replaced simultaneously. Selection at predetermined time intervals spreads selection pressure more evenly over the year. A strategy of selecting one boar every 52/NRBOARS weeks was incorporated in the model, where NRBOARS is number of boars used per year. The time a boar stayed in the herd depended on number of boars used simultaneously. Culling of a boar was postponed if no replacement boar was available. For founder boars a different strategy was chosen. In the foundation period, matings were unevenly distributed over the year. Founder boars, therefore, were allowed to do a maximum number of inseminations.

Mating of relatives was avoided; maximum inbreeding coefficient of potential offspring was 0.125. If no potential mates met this requirement, least related individuals were mated.

2.2 Alternatives

Little information is available on optimal size of nucleus lines. Using a deterministic approach based on assumptions from short-term selection theory, Naveau (1975) concluded that 100 sows were required to make pig breeding profitable. Enlarging the population to 200 sows enlarged profits. Naveau's assumptions are questionable but his conclusions serve as a starting point for further calculations. Effects of varying size of the sow herd around 100 sows on selection response and on inbreeding coefficient are evaluated in this paper. Four sizes of sow herds are examined: 25, 50, 100 and 150, which is the range considered to cover situations of practical interest. Size of the herd refers to total number of sow places available in breeding, gestation and farrowing houses.

According to Naveau (1975) 8 to 17 boars per year would be optimal. A smaller number of boars is undesirable because of an expected increase of inbreeding coefficient and the lengthening of generation interval. The range described by Naveau (1975) is examined in more detail; alternatives are 5, 10, 15 and 20 boars per year.

Each combination of number of sows and of boars is evaluated. Alternatives are characterized as number of sows/number of boars (e.g. 25/5, 25/10, etc.). Number of replicate runs per alternative is inversely proportional to number of sows, so that comparison of alternatives is based on a similar number of farrowings. Variance of means of replicates is approximately $2FV_A$ (Hill, 1977b), where F is average inbreeding coefficient and V_A is the additive genetic variance. Standard error of the average of these means is $\sqrt{(2FV_A/N)}$, where N is the number of replicates. With a total number of 500 sows, this standard error varies from .13 σ_A for alternative 25/20 to .42 σ_A for alternative 150/5. A substantial reduction of the standard error requires large numbers of replicates. Therefore, a total number of approximately 500 sows was assumed for all alternatives, resulting in 20, 10, 5 and 3 replicates for 25, 50, 100 and 150 sows.

Founder population sizes were equal to nucleus population sizes; number of founder sows applies to number of sows expected to farrow at least once. Founder animals were randomly selected from a large base population.

2.3 Parameters

The model was applied to a sire line with characteristics as in table 1. It was assumed that 67 percent of sows that entered the breeding piggery farrowed. Probabilities that sows were culled at weaning for conformation or

Table 1. General characteristics of nucleus breeding scheme.

General	
maximum number of parities per sow	5
length of suckling period (wks)	4.5
number of boars used simultaneously	3
size of pool of replacement boars	3
maximum relationship of partners at mating	0.125
Performance test	
minimum litter size at weaning	6
minimum start growth (0 to 23 kg, g.day^{-1})	300
maximum number of boars tested per litter	2
maximum number of gilts tested per litter	6
total number of testplaces in a division	50[a]
minimum index at end of test, boars	85
minimum index at end of test, gilts	65
percentage of boars culled for conformation	40
percentage of gilts culled for conformation	20
Sexual maturity	
percentage of boars culled for reproduction or conformation	40
percentage of gilts culled for conformation	20

[a] For 150 sows test capacity for gilts is enlarged to 60 places.

health problems were 10.0, 7.0, 7.5 and 10.0 percent for first, second, third, and fourth or greater parities. This culling was independent of the sow's performance for (re)production traits. Every week, a number of sows was selected for breeding. These sows came from the group of sows weaned in the previous week or from the pool of replacement gilts. Selection criterion was a performance index, that included production traits only.

Breeding goal (H) and selection index (I) were according to De Roo (1987):

$$H = 0.178 * A_{GR} - 0.05 * A_{FI} + 3.0 * A_{LEAN} \tag{4}$$

$$I_{boars} = 0.0212 * P_{GR} - 0.0004 * P_{FI} + 1.5548 * P_{LEAN} \tag{5}$$

$$I_{gilts} = 0.0357 * P_{GR} - 2.5965 * P_{SF} \tag{6}$$

where A_i,P_i: breeding values and phenotypes for trait i,
GR : growth rate 23 to 100 kg ($g.day^{-1}$),
FI : feed intake ($g.day^{-1}$),
LEAN : lean percentage,
SF : side-fat thickness (mm).

Potential breeding animals were performance tested. Boars were fed ad libitum, whereas gilts were kept on a restricted diet. Only the animal's own performance data were included in the index. Variables in (5) and (6) were deviations from batch means. Index values were standardized at a mean level of 100 with a standard deviation of 32. In presentation of results, attention will be focussed on production traits in boars. Genetic and phenotypic parameters of production traits in the base population are in table 2.

Lean percentage in boars was assumed to be estimated on live animals by means of modern equipment ($R^2 = 0.70$). Breeding values for lean percentage were assumed to be normally distributed, phenotypes were expressed on a scale with a minimum of 35 and a maximum of 75 percent (De Roo, 1987).

Selection of young breeding animals was a multi-stage process. At the end of the test a number of animals was culled for conformation and a relative mild selection on index was performed (table 1). At sexual maturity another number of animals was culled for conformation. In addition, a number of boars was culled because of a bad reproductive performance. For each sex, the animals with the highest indices among the remaining boars or sows were ultimately selected for breeding.

Table 2. Genetic and phenotypic parameters of production traits in the base population.

Trait	Mean	h^2	σ_p	Correlations[a]		
				GR	FI	LEAN
growth rate (GR, $g.day^{-1}$)	900	.25	88	--	.85	-.15
feed intake (FI, $g.day^{-1}$)	2 400	.25	200	.65	--	-.35
lean percentage (LEAN)	52	.45	2.5	-.10	-.30	--

[a] Upper triangle: genetic correlations, lower triangle: phenotypic correlations

2.4 Evaluation of selection response

Overall response was expressed in Dfl. using economic weights from eq. 4. Realized responses were compared to responses expected from selection index theory ($R_{init,e}$). Expected responses were calculated using genetic parameters from the base population.

$$R_{init,e} = 0.5 * (i_{boars} * \sigma_{I_{boars}} + i_{gilts} * \sigma_{I_{gilts}})/L \qquad (7)$$

where i : selection intensity,

σ_I: standard deviation of index,

L : mean age of parents at birth of offspring.

To minimize differences between expected and realized responses, realized generation intervals were used. The proportion of animals selected depended on number of animals that came off test weekly, number culled before sexual maturity and number of replacement animals needed weekly. Selection intensities came from tables for selection in finite populations (Becker, 1975).

An increase in genetic relationship between animals, which is inevitable in a closed population, is expected to lead to a decreased additive genetic variance (Falconer, 1981) and, thus, to a diminished response to selection. For this reason, an exponential curve (W.J. Koops, personal communication) was fitted to cumulative response (R_{cum}) for each replicate:

$$R_{cum} = R_{init}*(YEAR-INTCPT)*\exp(-BEND*(YEAR-INTCPT)) \quad (8)$$

Parameter R_{init} is the initial response per year, BEND is the change in response as time proceeds, INTCPT is the intercept of the curve on the x-axis. INTCPT was calculated from data of year 3 to year 10 by linear extrapolation. Parameters R_{init} and BEND were estimated after a logarithmic transformation:

$$\ln(R_{cum}/(YEAR-INTCPT)) = \ln(R_{init})-BEND*(YEAR-INTCPT) \quad (9)$$

3. RESULTS AND DISCUSSION

3.1 Characteristics of the herd

Herd characteristics are in tables 3 to 5. Number of sows and age distribution of animals stabilized after 3 years. Therefore, results are presented as means over years 4 to 25. Results are averaged over boar alternatives within each sow alternative because number of boars did not alter these characteristics systematically.

Actual numbers of sows present were close to intended numbers (table 3). Average number of farrowings per sow per year varied between 2.18 for 25 sows to 2.20 for 150 sows and number of inseminations per farrowing was between 1.27 and 1.25. Percentage of first parity sows was high in each

Table 3. Percent distribution of farrowings per parity and actual number of sows present.

Alter-native	Parity 1	2	3	4	5	Number of sows
25/*	63.3	19.7	9.1	5.1	2.9	26.1
50/*	59.6	20.1	10.4	6.2	3.7	50.3
100/*	56.7	20.7	11.3	7.0	4.4	101.1
150/*	53.8	21.4	12.0	7.8	5.0	152.4

case, but decreased as population size increased. The larger the population, the more regular replacement gilts became available, and this enabled stronger selection in these gilts (table 4). As a result, the difference in index between average replacement gilts and selected females increased. This explains the diminishing contribution of index as a reason for culling in sows and the relative decrease in number of sows culled per year (table 4). In a larger population, selected gilts have a smaller probability of being culled for a low index in later life. Table 4 does not give optimal parity distributions with respect to genetic improvement, because indices were not corrected for genetic trend. Such a correction would lead to an increased contribution of younger sows. The correction would be most important for larger populations, because genetic improvement is largest in those herds. The change in parity distribution with increasing population size, therefore, is overestimated.

Table 4. Percent distribution of number of culled sows per reason for culling.

Reason for culling	Gilts[a] Alternative				Sows[b] Alternative			
	25/*	50/*	100/*	150/*	25/*	50/*	100/*	150/*
failure to breed	0.6	0.5	0.5	0.4	0.9	1.0	1.2	1.3
barren	1.1	.9	0.9	0.8	1.6	1.8	2.1	2.4
no oestrus	17.4	15.3	14.3	13.2	20.8	23.5	26.1	28.9
abortion or late oestrus	1.3	1.1	1.1	1.0	2.0	2.3	2.6	2.9
age					4.5	6.3	7.8	9.4
leg problems	27.7	26.8	26.2	25.7	14.0	15.0	15.3	16.0
index	51.6	55.3	57.0	58.8	56.2	50.0	44.8	39.1
Total number culled per year	96	199	406	625	36	66	125	180

[a] end of test to first parity

[b] first to fifth parity

Average age of sows at culling increased slightly as population size increased (table 5). Average number of litters per sow increased by about 20 percent, however, leading to a relative higher contribution of individual sows to the next generation of offspring.

Table 5. Characteristics of culled sows.

Alternative	Age at culling (years)	Average no. of litters	Number of piglets born per sow per year	Number of piglets weaned per sow per year
25/*	1.40	1.58	16.7	13.5
50/*	1.45	1.68	17.8	14.4
100/*	1.49	1.77	18.8	15.1
150/*	1.52	1.86	20.0	16.0

Litter size at birth in first parity sows increased by 0.4 piglet per litter in 25 years. This is due to mild selection on litter size at the start of the performance test (table 1) and to the higher probability for gilts from larger litters of being selected because number of tested gilts per litter increased with litter size. Parameters used for ovulation rate and prenatal survival produced a result similar to the previous model in which litter size at birth was simulated as an independent trait (De Roo, 1987). Further investigation of the nature of prenatal survival is justified (Bolet, 1986). The same applies to genetic parameters of components of litter size.

Characteristics of breeding boars are in table 6. Only results of alternatives with 25 and 150 sows are presented. With a small number of sows, boars could not always be replaced at the desired time, because replacement boars were not always available. Thus, some boars stayed relatively long in the herd. When population size increased, fluctuations in number of weeks in service decreased. Number of matings per boar varied considerably as a result of replacement of boars at regular time intervals. Random fluctuations in number of sows in heat contributed to fluctuations in number of matings per boar. Fluctuations in number of matings increased with time due to the policy of avoidance of mating of relatives. If a boar was selected that was relatively closely related to sows in the herd, it performed

Table 6. Characteristics of breeding boars.

Alter-	Boars per year			Matings per boar			Weeks in service		
native	mean	min	max	mean	min	max	mean	min	max
25/5	5.0	4	6	14.3	0	43	31.1	25	37
25/10	10.0	8	11	7.2	0	21	15.6	6	29
25/15	14.8	10	17	4.9	0	21	10.5	3	32
25/20	18.9	12	23	3.8	0	23	8.3	0[a]	31
150/5	5.0	5	5	83.9	17	187	31.2	31	32
150/10	10.0	10	10	42.1	6	89	15.6	15	16
150/15	15.0	15	15	28.0	12	59	10.4	10	11
150/20	20.0	20	20	21.0	11	29	7.8	7	8

[a] Boar was culled in the same week as it was selected.

few inseminations in the time period allowed. The opposite was true for boars with a relatively low genetic relationship with sows.

On average, 3.59 gilts and 1.76 boars were tested per litter. Total number of boars tested per year increased from 99 for 25 sows to 592 for 150 sows. Number of gilts tested was about twice as high. From 3.2 to 4.6 percent of available gilts and 2.4 to 3.4 percent of available boars could not be tested because of insufficient test capacity with smallest percentages applying to alternatives with 100 or 150 sows.

3.2 Selection response

3.2.1 Response for individual traits

Mean levels of production traits in year 25 are in table 7. Response for lean varied from 6.65 percent for alternative 25/20 to 13.99 percent for 150/15. Response for growth rate increases from 93 $g.day^{-1}$ for 25/20 to 181 $g.day^{-1}$ for 150/15. Relative response for lean percentage and growth rate was in agreement with expectations for alternatives with 25 sows. When overall response increased, the relative contribution of growth rate increased greater than expected. Because of the manner in which lean percentage was simulated with an upper biological limit (75 percent), its phenotypic variance diminished and emphasis in index selection was shifted

Table 7. Means and their standard errors (sem) over replicates for production traits in year 25.

Alternative	Growth ($g.day^{-1}$) mean	sem	Feed intake ($g.day^{-1}$) mean	sem	Lean percentage mean	sem
25/5	1 005	9	2 414	22	60.76	.27
25/10	986	7	2 382	16	60.77	.20
25/15	999	6	2 398	15	59.46	.22
25/20	993	5	2 402	10	58.65	.22
50/5	1 021	12	2 394	35	63.44	.34
50/10	1 027	8	2 385	15	63.32	.25
50/15	1 036	9	2 430	17	62.30	.21
50/20	1 026	6	2 379	18	61.84	.23
100/5	1 043	9	2 400	32	64.40	.39
100/10	1 037	8	2 374	29	64.60	.26
100/15	1 060	11	2 415	22	64.66	.26
100/20	1 066	8	2 436	14	64.63	.14
150/5	1 063	18	2 419	21	65.70	.09
150/10	1 060	7	2 384	4	65.97	.50
150/15	1 081	20	2 408	17	65.99	.31
150/20	1 074	16	2 432	18	65.11	.17

to other traits as lean percentage increased. This phenomenon is also illustrated by response of feed intake. A negative response for feed intake was expected from selection theory. For alternatives with 100 or 150 sows, however, response was negative in the early years of selection, but often became positive in later years. These results illustrate that selection index theory does not provide optimal weighing factors for long-term response to selection when a trait with a maximum is included in the breeding goal.

3.2.2 Overall response: short-term effects

Values of R_{init} and INTCPT (eq. 8), averaged over replicates, are in table 8. Variation in INTCPT reflects differences in the founder population, which is the result of the random selection of founder animals from a large base population.

Values of R_{init} showed that differences between sow alternatives were larger than differences between boar alternatives within sow alternatives. (table 8, figures 1 and 2). Differences in response between boar alterna-

Table 8. Characteristics of response curves: intercepts of curves on x-axis (INTCPT), expected ($R_{init,e}$) and realized (R_{init}) initial responses per year, deviations from linearity (BEND) and its standard error over replicates (sem_{BEND}), expected[a] ($R_{cum,e}$) and realized (R_{cum}) cumulative responses up to year 25 and standard error of R_{cum} ($sem_{R_{cum}}$) over replicates (response in Dfl.).

Alternative	INTCPT	$R_{init,e}$	R_{init}	BEND	sem_{BEND}	$R_{cum,e}$	R_{cum}	$sem_{R_{cum}}$
25/5	1.85	2.95	1.95	.0001	.0042	67.93	45.60	1.43
25/10	2.32	2.51	2.15	.0067	.0019	57.64	42.30	1.31
25/15	2.20	2.10	2.00	.0056	.0025	48.28	40.36	.87
25/20	2.04	1.79	1.74	.0037	.0031	41.21	37.24	1.15
50/5	2.53	3.40	2.98	.0078	.0036	78.21	56.63	2.19
50/10	1.72	3.07	2.65	.0027	.0012	70.62	58.17	1.53
50/15	1.94	2.76	2.74	.0069	.0024	63.44	53.93	1.16
50/20	2.27	2.50	2.52	.0038	.0020	57.46	52.77	.92
100/5	2.07	3.88	3.39	.0096	.0033	89.13	62.60	2.04
100/10	1.72	3.62	2.97	.0027	.0011	83.26	65.03	2.09
100/15	1.70	3.38	3.27	.0061	.0026	77.73	66.13	1.25
100/20	1.76	3.18	3.05	.0031	.0013	73.22	65.92	.80
150/5	1.49	4.11	4.25	.0152	.0025	94.49	69.90	2.54
150/10	1.84	3.86	3.66	.0077	.0018	88.89	71.31	4.51
150/15	1.73	3.69	3.68	.0061	.0018	84.91	74.47	2.80
150/20	1.77	3.52	3.32	.0050	.0007	80.93	68.77	2.24

[a] 23 years of selection were assumed.

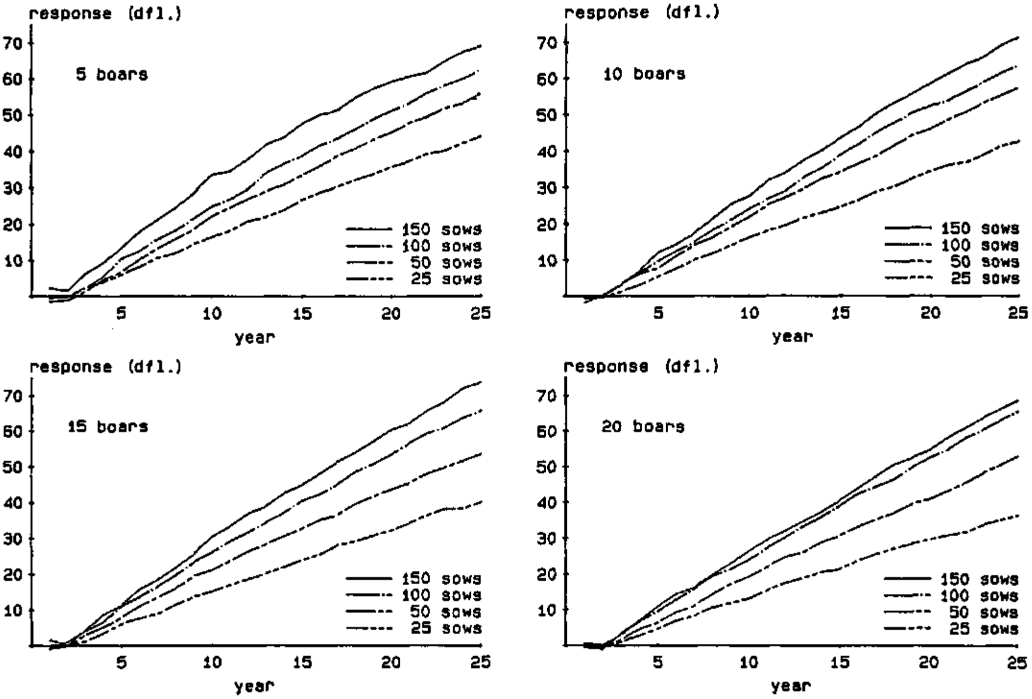

Figure 1. Effects of variation in size of the sow herd on selection response over time, for different numbers of boars used per year.

tives were expected to decrease with increasing population size because differences in selection intensity decreased (table 9): for 25/20 37 percent of selection intensity of 25/5 was expected and for 150/20 72 percent of selection intensity of 150/5 was expected. Realized differences in response, however, were less than expected. This was mainly due to a less than expected response for boar alternatives with intense selection (5 or 10 boars annually).

An explanation for small differences between boar alternatives is given by Hill (1976, 1977a). Expected responses (eq. 7) were calculated under the assumption that observations upon which selection was based were independent. When 3 boars are used simultaneously with a low boar turn-over rate (table 6), however, observations on offspring are correlated. As a result, selection intensities used are overestimated. This overestimation is largest, when number of families is small and increases with increased selection intensity (Hill, 1976). All boar alternatives used 3 boars simultaneously. However, boar turn-over rates increased when number of boars used per

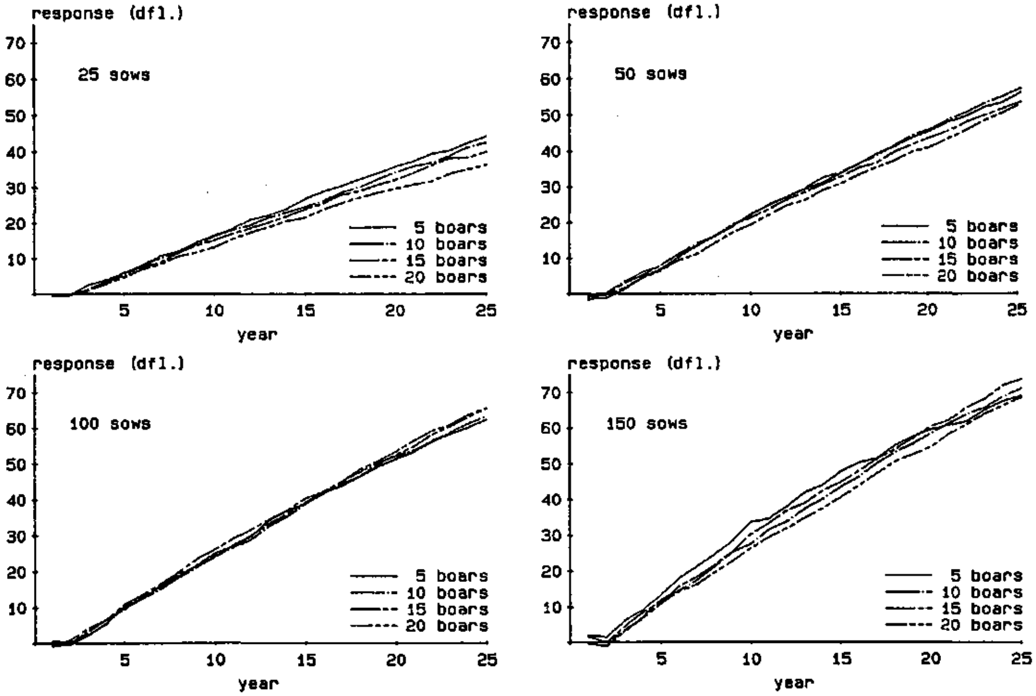

Figure 2. Effects of variation in number of boars used per year on selection response over time, for different numbers of sows.

Table 9. Generation intervals (L, in years) and selection intensities (i) used in calculations of expected responses to selection (m= male, f= female).

Alternative	L_m	L_f	i_m	i_f	Alternative	L_m	L_f	i_m	i_f
25/5	1.39	1.31	1.404	.816	100/5	1.38	1.37	2.017	.885
25/10	1.21	1.31	1.003	.816	100/10	1.21	1.38	1.707	.885
25/15	1.14	1.31	.725	.816	100/15	1.15	1.39	1.507	.885
25/20	1.11	1.31	.525	.816	100/20	1.12	1.37	1.356	.885
50/5	1.38	1.35	1.702	.857	150/5	1.39	1.39	2.184	.898
50/10	1.21	1.34	1.350	.857	150/10	1.21	1.41	1.871	.898
50/15	1.15	1.35	1.117	.857	150/15	1.15	1.42	1.708	.898
50/20	1.12	1.35	.936	.857	150/20	1.12	1.41	1.567	.898

year increased, which means that more sires contributed to the group of boars from which replacement boars were selected. Selection intensities from table 9 more closely reflect reality for these alternatives.

Eq. 7 also assumed constant variance over time. Selection, however, invokes linkage disequilibrium. Because of selection of parents, variance among offspring is reduced. As a result response to subsequent selection is diminished (Bulmer, 1971, 1976; Mueller and James, 1983b; Robertson, 1977). Linkage disequilibrium effects are largest at high selection intensities. These phenomena explain why deviations from expectations were larger when selection was more intense.

3.2.3 Overall response up to year 25

Response curves are in figures 1 and 2. Eq. 8 fitted these curves acceptably: the residual standard deviation, expressed as a percentage of cumulative response in year 25, varied from 1.2 percent for 150/20 to 5.1 percent for 25/20. Cumulative responses up to year 25 were considerable less than expected from linear extrapolation of expected initial responses (table 8). This was partly due to overestimation of response by eq. 7. This does not explain, however, the change in ranking of boar alternatives compared with short-term results.

Parameter BEND (eq. 8) indicates whether response curves deviate from linearity. Values of BEND were small but positive (table 8), indicating a reduction in response with time. Values of BEND were largest when selection was most intense, leading to a reduction in advantage or even to a disadvantage of alternatives with 5 boars annually, when response up to year 25 was observed.

With a small number of boars, increase in genetic relationship between animals was fast (fig. 3). Consequently, the between-sire and between-dam variance components were reduced relative to a population of unrelated animals (Hill, 1976). Within-family variance was also reduced as the inbreeding coefficient increased (Thompson, 1977; Sörensen and Kennedy, 1984). As a result, variance among offspring was reduced and response to subsequent selection was diminished.

For 150/5 values of BEND were larger than for other sow alternatives with the same number of boars, while inbreeding levels were similar for these alternatives (table 10, figure 3). This was due to the intense selection practiced for 150/5: the higher the initial selection intensity and the

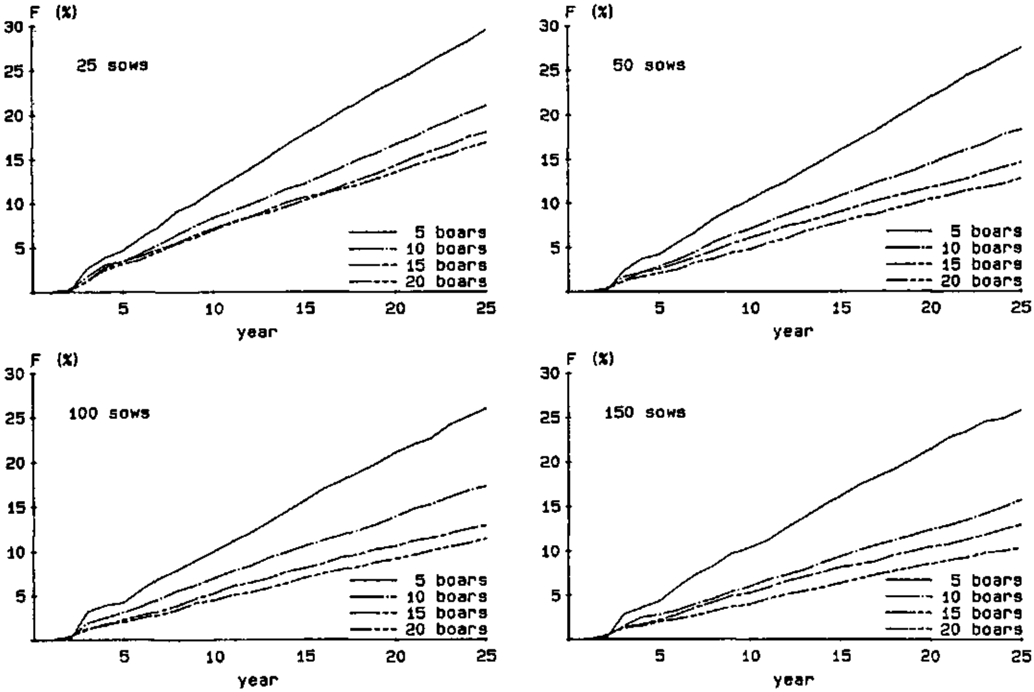

Figure 3. Changes in inbreeding coefficient (F) over time as a function of number of sows and number of boars used per year.

Table 10. Means and standard errors of the inbreeding coeffient (F) over replicates, expected (ΔF_e) and realized (ΔF_r) yearly increases in F and realized effective population sizes (NE_r).

Alternative	F	sem_F	ΔF_e	ΔF_r	NE_r	Alternative	F	sem_F	ΔF_e	ΔF_r	NE_r
25/5	29.5	.3	1.56	1.46	36	100/5	26.0	.7	1.37	1.21	42
25/10	21.0	.3	1.01	.99	53	100/10	17.3	.2	.80	.77	66
25/15	18.0	.2	.79	.84	63	100/15	12.9	.3	.58	.57	91
25/20	16.9	.2	.69	.78	68	100/20	11.4	.4	.47	.49	104
50/5	27.3	.3	1.44	1.33	39	150/5	25.7	.9	1.33	1.21	42
50/10	18.2	.3	.88	.83	63	150/10	15.7	.3	.77	.70	74
50/15	14.5	.3	.66	.65	81	150/15	12.9	.4	.55	.56	91
50/20	12.7	.1	.54	.56	93	150/20	10.3	.1	.43	.43	116

smaller the number of families, the more dramatic is the reduction in selection intensity when the genetic relationship between animals increases (Hill, 1976).

To provide a more general idea about the relation between population size and selection response, a curve was fitted to responses attained with different numbers of sows for every boar alternative. Koops (personal communication) suggested use of the Michaelis-Menten curve (France and Thornley, 1984):

$$R_{cum} = R_{lim} * NRSOWS / (NRSOWS_{50\%} + NRSOWS) \quad (10)$$

where R_{lim} is maximum attainable selection response when population size is infinite and $NRSOWS_{50\%}$ is population size with which 50 percent of this maximum can be attained. This curve gave a good fit without systematic errors; residual standard deviation was 3.3 percent of R_{lim}, on average. Values of R_{lim} and $NRSOWS_{50\%}$ with 95 percent confidence intervals are in table 11. R_{lim} was largest when 15 boars were used annually. Advantages compared to 10 and 20 boars, however, were small. Use of 5 boars provided inferior results. Relative responses, expressed as a percentage of the limit to be attained with 15 boars, are in figure 4. Optimum number of boars depended on number of sows: when population size increased, optimal number of boars increased to 15.

Table 11. Characteristics of curves that describe cumulative response up to year 25 as a function of number of sows for different boar alternatives: maximum responses (R_{lim}) to be attained with an infinite number of sows, number of sows ($NRSOWS_{50\%}$) needed to attain 50 percent of this maximum and 95 percent confidence intervals.

number of boars	R_{lim} (Dfl.)	confidence interval	$NRSOWS_{50\%}$	confidence interval
5	75.81	63.97-87.64	16.96	4.87-29.06
10	81.18	69.46-92.90	22.01	9.48-34.53
15	88.34	76.70-99.98	30.95	17.47-44.42
20	84.17	73.19-95.15	30.42	17.19-43.64

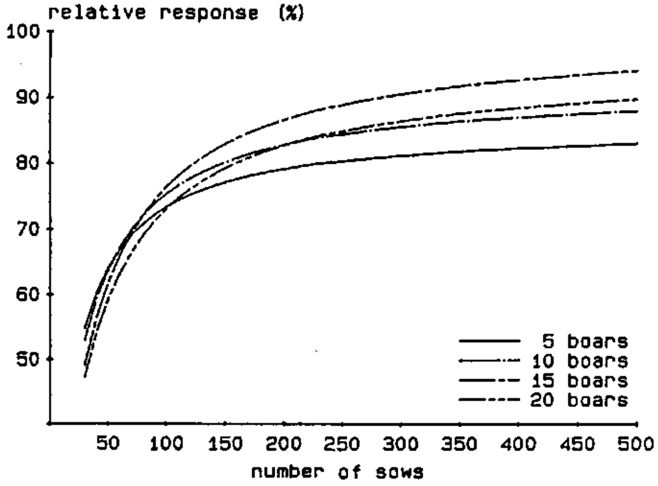

Figure 4. Relative cumulative response up to year 25 as a function of number of sows and number of boars used per year. Maximum response with an infinite number of sows and 15 boars annually equals 100%.

3.2.4 Effect of breeding scheme on within-line variance

In a random mating population with no selection, additive variance is expected to follow (Falconer, 1981):

$$V_{A_t} = (1 - F_t) * V_{A_0} \qquad (11)$$

where V_{A_t} : additive genetic variance at time t,

V_{A_0} : additive genetic variance in base population,

F_t : inbreeding coefficient at time t.

In table 12, reductions in average within-replicate additive genetic variance are compared to expected reductions in a random mating population. To reduce random year effects, averages over years 23 to 25 are presented. For lean percentage, growth rate and feed intake, realized reductions were considerably larger than expected from eq. 11, especially for alternatives with few boars annually.

Two trends are visible in table 12. On one hand, reductions in additive genetic variance decreased, when effective population size increased. Compared at the same number of boars, reductions for alternatives with 50 sows were less than for alternatives with 25 sows. On the other hand, when

Table 12. Expected and realized reductions in within-line additive genetic variance, expressed as a percentage of the initial additive genetic variance.

Alternative	Expected	Realized			Alternative	Expected	Realized		
		Growth	Feed intake	Lean pct			Growth	Feed intake	Lean pct
25/5	28.2	41.5	39.7	37.6	100/5	25.1	34.3	36.5	36.1
25/10	20.2	28.0	27.8	29.6	100/10	16.8	24.1	23.1	24.5
25/15	17.5	24.1	22.0	21.3	100/15	12.5	14.6	14.7	20.3
25/20	16.3	21.4	23.1	25.5	100/20	10.9	16.0	16.6	19.6
50/5	26.3	30.6	31.1	36.4	150/5	24.8	36.7	38.1	41.3
50/10	17.7	25.4	27.8	29.6	150/10	14.9	25.4	25.5	24.8
50/15	14.0	17.4	16.6	21.7	150/15	12.4	20.1	19.6	21.7
50/20	12.1	18.7	19.0	17.4	150/20	10.0	17.4	12.3	14.5

selection intensities increased, reductions in additive genetic variance also increased. For alternatives with 100 sows, reductions were less than for alternatives with 150 sows. Enlarging the effective population size, thus, was not sufficient to counteract the increased influence of selection on the variance. These results underline results described in the previous section: genetic change through a breeding program is not only dependent on selection intensity, but also on effective population size.

3.2.5 Effect of breeding scheme on between-line variance

Standard errors of means over replicates showed that considerable variance existed between replicates (tables 7, 8). Drift is a major cause of variance between replicates (Hill, 1977b; Sörensen and Kennedy, 1983). When number of observations included in the mean is large, error variance due to sampling can be ignored and expected variances of means can be calculated according to Sörensen and Kennedy (1983):

$$V_{P_t} = 2 * F_{t+1} * V_{A_0} \tag{12}$$

where V_{P_t} : variance of means at year t,

F_{t+1} : inbreeding coefficient at year t+1.

In table 13, expected and realized standard deviations of means are listed. Realized values were again averaged over years 23 to 25.

For growth and feed intake, expected and realized standard deviations were close. When population size increased, standard deviation of means decreased. Deviations from expectation, however, increased because of a smaller number of replicates.

For lean percentage, realized standard deviations of means were below expectations because of the assumed distribution for the trait (De Roo, 1987): at the approach of the upper biological limit (75 percent) phenotypic variance diminished. Alternatives with highest mean levels of lean percentage (150/*), therefore, showed largest deviations from expectations.

Variances of means showed that confidence intervals for expected response in a single line were relatively wide and there was considerable overlap between alternatives.

Table 13. Expected (sd_e) and realized (sd_r) standard deviations of replicate means for production traits.

Alternative	Growth		Feed intake		Lean percentage		Alternative	Growth		Feed intake		Lean percentage	
	sd_e	sd_r	sd_e	sd_r	sd_e	sd_r		sd_e	sd_r	sd_e	sd_r	sd_e	sd_r
25/5	34	38	77	92	1.29	1.19	100/5	32	21	72	63	1.21	.79
25/10	29	31	65	67	1.09	.93	100/10	26	14	59	57	.99	.66
25/15	26	27	60	67	1.01	.87	100/15	22	21	51	46	.85	.73
25/20	26	22	58	41	.98	.97	100/20	21	17	48	34	.80	.24
50/5	33	39	74	103	1.24	1.16	150/5	32	36	72	52	1.20	.23
50/10	27	24	60	48	1.01	.78	150/10	25	19	56	6	.94	.92
50/15	24	26	54	53	.90	.73	150/15	22	29	51	23	.85	.53
50/20	22	18	50	53	.85	.69	150/20	20	31	45	36	.76	.28

3.3 Inbreeding coefficient (F)

Number of boars had the largest influence on level of F (table 10, figure 3), as expected from theory (Wright, 1931). Number of sows had a small effect when number of boars remained small. Realized values of the yearly relative increase of F (ΔF_r) were calculated from Falconer (1981):

$$\Delta F_r = (F_t - F_{t-1}) / (1 - F_{t-1}) \tag{13}$$

Expected yearly relative increases of F were calculated according to Hill (1972):

$$\Delta F_e = (1/N_m + 1/N_f) / (8 * L^2) \tag{14}$$

where L : length of generation interval,

N_m, N_f : number of males and females used for breeding during a year.

Realized values of ΔF were generally close to expectations. Deviations from expectation depended on number of boars. For a small number of boars, ΔF_r was smaller than ΔF_e; with 20 boars the opposite was true. This pattern applied to all sow alternatives.

Selection leads to unequal contributions of animals to subsequent generations. This causes an increase in F relative to random mating (Robertson, 1961). Avoidance of mating of relatives was expected to oppose this effect of selection. This opposing effect was strongest when number of boars was small, ΔF_r was smaller than ΔF_e in that case (table 10). With a small number of boars, the rate of increase in F was highest, which means that the probability that a mating must be prohibited was largest. Avoidance of mating of relatives, thus, can offer a contribution in a strategy that aims at a limited rise of the inbreeding coefficient, especially when effective population size is small. Magnitude of the effect needs further investigation.

3.4 General discussion

The selection policy that will yield optimum results depends on the genetic model. Very intense selection would be justified with free recombination, a low number of loci and high frequencies of desirable genes (Robertson, 1970b). A similar conclusion holds when differences in gene effects between loci are large. In this paper, breeding values of traits were simulated using normal deviates. This requires a large number of loci and intermediate gene frequencies. Selection then hardly changes the average gene frequency and the equilibrium additive genetic variance (Falconer, 1981). With low initial gene frequencies, selection causes a relative large increase in additive genetic variance and response to selection will be higher than expected from a model with normal deviates. With high initial frequencies, selection will decrease additive genetic variance and response will be lower than expected from a model with normal deviates. Summarizing, results apply to traits affected by a considerable number of loci, with intermediate gene frequencies, small differences in gene effects between loci and no epistasis.

In a sire line, emphasis is on improvement of additive genetic values. The level of F is relevant to breeders because it affects the additive genetic variance. Direct inbreeding depression effects on production traits are less important in a sire line because a loss in heterozygosity will be regained in hybrid slaughter pigs. Through its effect on fertility, however, inbreeding depression might also affect selection response indirectly. Direct and indirect effects of inbreeding depression need further investigation.

Intense selection in boars offered limited advantages for response in the first 5 to 10 years of selection (figure 2). These advantages were smaller than expected from selection index theory (table 8), because assumptions of independent observations and constant variance were violated. As stated by Bulmer (1971, 1976) and Hill (1976, 1977b), selection theory should not ignore linkage disequilibrium. Comparison of alternative breeding schemes should include a correction for the amount of linkage disequilibrium caused by each breeding scheme. The equilibrium additive genetic variance (Fimland, 1979) should be used in the calculation of expected response to selection. When number of families is small, as in many practical situations selection intensities used should also be corrected for family size, except when available family information is included in the index and when selection intensities are based on number of families (Hill, 1976, 1977a).

As the time period included in the evaluation of a breeding scheme increased, the optimal number of boars used per year also increased (figure 2). Twenty five years after the start of the breeding program, differences between boar alternatives considered in this study were small. Use of 15 to 20 boars per year gave good response, maintained additive genetic variance at an acceptable level and limited the rate of increase in F. The latter aspect is especially important because inbreeding depression was not considered in this paper. Responses given in table 8 are based on additive effects only and should, therefore, be regarded as upper limits. Inclusion of inbreeding depression effects would diminish response most severely for alternatives that cause a high rate of increase in F.

A comparison of maximum attainable responses with each number of sows shows, that for the breeding scheme studied, 52, 66, 75 and 84 percent of maximum response with an infinite number of sows was attained with 25, 50, 100 and 150 sows (tables 8 and 11). Further increases in response require relatively large increases in number of sows. The relative benefit of enlarging the population was larger than expected from ratios of expected maximum responses. With 25, 50 and 100 sows, 61, 78 and 89 percent of response with 150 sows was attained, expected relative responses were 72, 83 and 94 percent (table 8). Because optimal annual number of boars increased with population size, the validity of the assumption of a large number of families also increased and the ratio of realized and expected maximum responses narrowed when population size increased. Realized maximum responses, however, were only 70 to 80 percent of expected maximum responses.

Drift caused considerable differences in responses between replicates. Standard deviation of response in a single line equals the standard error of the mean (table 8) multiplied by the square root of number of replicates. These standard deviations were quite large and should be considered in the evaluation of breeding schemes. Standard deviations, however, were small compared to differences in means between sow alternatives, especially when number of sows was small. Splitting of the population into independent sublines, therefore, is unadvisable, unless total number of sows is very large.

Heritabilities for traits under selection were moderately to high in this study (table 2). For traits with a lower heritability, selection would be less effective, the amount of linkage disequilibrium would be less and rate of increase in F would be more conform expectations for a situation of random mating. Realized responses, therefore, would be closer to expectations from short-term theory, and relative response with a small number of sows would be higher than in the present study. This conclusion, however, is only valid when mass selection is practiced, with own performance data as the only source of information.

In this study, selection was based on own performance data. Including family information in the index should improve accuracy of selection and, thus, initial response. The amount of linkage disequilibrium, however, will also increase, reducing the advantage of higher accuracy. Secondly, response will diminish faster because increases in relationship between animals will be faster. Short-term selection theory, thus, overestimates benefits of including family information in a selection index.

Response curves as a function of size of the sow herd and annual number of boars (figure 4) will change when family information is used. In a larger population, number of offspring per boar will be larger and the increase in accuracy will be larger. Effects of including family information will be more dramatic when initial accuracy is low, as for example for fertility traits. For a sow line, therefore, increase of response, expected by enlarging the population, might be larger than suggested by figure 4.

A reduction of culling percentages used in this study leads to an increase in selection intensity because of an increase in number of animals available for selection. Initial response is expected to be improved, but response curves will show a stronger curvilinear trend than in figures 1 and 2. Improvement of initial response is most important if number of sows is small because increase of selection intensity is largest in this situation. Optimal annual number of boars will increase for those herds. Enlarging number of animals tested per litter has similar effects.

Selection responses also depend on number of boars used simultaneously. An increase in this number is expected to lead to a decrease in response because of a lengthening of the generation interval, but also to an increase in the possibilities of avoidance of mating of relatives and, thus, to a lower rate of increase in F. The net effect on selection response is not clear.

Further investigations towards effects of changes in the breeding scheme on levels of absolute and relative responses are justified.

APPENDIX

Because selection for litter size has often been unsuccessful, Johnson et al. (1985) advocated selection for its components, ovulation rate and prenatal survival. Van der Steen et al. (1986) showed that the distribution of litter size is skewed toward the right. An explanation lays in a decrease of prenatal survival at an increasing ovulation rate. Ovulation rate exhibits a normal distribution (Blichfeldt and Almlid, 1982; Van der Lende et al., 1987) with a standard deviation that varies between 2.4 and 3.4 (Legault and Gruand, 1981; Blichfeldt and Almlid, 1982; Johnson et al., 1984; King and Williams, 1984; Van der Lende et al., 1987). Reported values of the standard deviation might be biased downward, for two reasons. A small number of ovulations is not sufficient to establish pregnancy (Polge et al., 1966) and might thus not be included in analyzed data. High ovulation rates are relatively scarce and can accidently be absent when a limited number of sows is examined. For these reasons, a standard deviation of 3.5 was chosen. Heritability of ovulation rate was chosen to be 0.3 (Bradford, 1969; Land and Falconer, 1969; Legault and Gruand, 1981; Johnson et al., 1985; Neal and Johnson, 1986). In a review, Bolet (1986) concluded that prenatal survival showed no within-breed additive variance. Therefore, only phenotypic values were simulated for the trait.

Wrathall (1971) and Schoenmaker and Van der Lende (1987) came to a similar linear relation of ovulation rate (OR) and prenatal survival (PS):

$$PS = 108 - 2.62 * OR \qquad (1)$$

Legault and Gruand (1981), Sasaki and Johnson (cited by Johnson et al., 1985) and Leymaster et al. (1986) found a curvilinear relationship. A curve, that approaches eq. 1 and deviates from it at higher ovulation rates is reasonable from a physiological standpoint: it expresses approach to a biological limit to number of piglets born. Koops (personal communication) suggested use of the Michaelis-Menten curve (France and Thornley, 1984):

$$PS = OR_{50\%} / (OR + OR_{50\%}) \qquad (2)$$

$OR_{50\%}$ depends on parity and equals number of ovulations at which 50 percent of the embryo's survive. Equation 2 was used to determine the probability that an embryo survived up to birth.

Bolet (1986) stated 70 percent as a base level of prenatal survival. Several experiments reported about mean ovulation rate in gilts (e.g. Blichfeldt and Almlid, 1982; Johnson et al., 1984; King and Williams, 1984; Van der Lende et al., 1987). Little is known, however, about parity effects on levels of ovulation rate and prenatal survival. For this reason, values of OR and $OR_{50\%}$ were chosen to keep resulting litter sizes in agreement with De Roo (1987), mean values of OR for gilts and first to fourth parity sows were 14.0, 15.1, 16.3, 17.0 and 17.0; values of $OR_{50\%}$ were 34.27, 36.97, 38.95, 40.63 and 40.63. A minimum number of 4 ovulations was assumed necessary to establish pregnancy (Polge et al., 1966).

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Chapter 4

STUDIES ON BREEDING SCHEMES IN A CLOSED PIG POPULATION

2. Mating policy

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ABSTRACT

A stochastic model was used to examine the effect of mating policy on selection response and inbreeding coefficient in a closed swine herd. Effects of changes in number of boars used simultaneously were evaluated for two sizes of the sow herd, 25 and 100, and two numbers of boars used per year, 5 and 20. Number of boars used simultaneously varied from 1 to 10. Maximum avoidance of mating of relatives was compared to no avoidance.

Under the additive genetic model followed, cumulative response over a period of 25 years was generally highest with 3 boars used simultaneously and no avoidance of mating of relatives. With avoidance of mating of relatives, number of offspring of sires with few relatives was increased. These sires probably were not as good genetically as sires with many relatives, because selection was on phenotype alone. Mating of genetically diverse animals reduced the additive genetic variance among offspring. Unequal numbers of offspring of sires also contributed to a lower additive genetic variance and, thus, to a lower response to selection for alternatives with avoidance of mating of relatives.

Avoiding mating of relatives initially postponed the increase of the inbreeding coefficient (F). Rate of increase in F after year five, however, was rather independent of mating policy. Differences in F in year 25 were considerable and ranged from 2.1 percent for 100 sows, 20 boars annually and 10 boars at a time to 6.9 percent for 100 sows, 5 boars annually and 3 boars at a time. The risk of an unexpected high level of F was also higher when there was no avoidance of mating of relatives.

1. INTRODUCTION

Selection response and rate of increase in inbreeding coefficient in a finite population depend on population size, selection method and mating policy. Mating policy includes the choice whether and to what extent mating of relatives should be avoided. It also implies choice of number of boars to be used simultaneously for breeding.

Avoidance of mating of relatives is often practiced in pig nucleus breeding. Wright (1921) stated that a system that avoids mating of relatives as much as possible minimizes the rate of increase in inbreeding coefficient. Kimura and Crow (1963) showed that circular mating systems resulted in a slower approach to homozygosity. Robertson (1964) generalized the results of Kimura and Crow (1963) and concluded that mating of close relatives leads to greater initial inbreeding but also to a lower final rate of approach to the limit.

Robertson's theory implies that avoidance of mating of relatives is not beneficial in the long term. The time period of interest to animal breeders, however, is limited to 10 or possibly 20 generations. This means that breeders are less interested in the limit than in intermediate periods and a system of avoidance of inbreeding might be of value to them.

Theory of avoidance of inbreeding (e.g. Robertson, 1964; Cockerham, 1970; Jacquard, 1971) often disregarded selection. In pig nucleus breeding, however, both selection and inbreeding coefficient are relevant and, in addition, affect each other. Selection increases the rate of increase in inbreeding coefficient (Roberton, 1961; Belonsky and Kennedy, 1987; De Roo, 1987b) and an increase in inbreeding coefficient is accompanied by a decrease in additive genetic variance available for selection (Falconer, 1981).

Number of boars used simultaneously determines possibilities of avoidance of mating of relatives and also affects selection response because it influences additive genetic variance available for selection at a given moment. Generation interval in males depends on the ratio of number of boars used simultaneously to number of boars used per year. At a fixed annual number of boars, a decrease in number of boars used simultaneously leads to decrease in generation interval, which is favourable with respect to selection response, but unfavourable from the point of view of limiting inbreeding (Hill, 1972).

Determination of an optimum mating policy for the practical situation of a pig nucleus is complicated. The aim of this paper was to study effects of different mating policies on selection response and inbreeding coefficient over time. A model of a closed pig population (De Roo, 1987a) was used for this purpose.

2. MATERIAL AND METHODS

2.1 Model

The model described by De Roo (1987a,b) measured changes in production and reproduction traits and inbreeding coefficient over 25 years of selection in a closed swine herd. Growth rate (23 to 100 kg), feed intake, lean percentage, litter size and interval from weaning to oestrus were incorporated in the model because of their economic relevance to pig breeders. The model included overlapping generations, continuous mating and farrowing and weekly selection of boars and sows. Week was the unit of time.

De Roo (1988) argued that an infinitesimal model, in which traits are affected by an infinite number of unlinked loci of small effect each, would provide useful information to pig breeding. An additive, infinitesimal model was used in this paper, epistatic effects were ignored. Breeding values were generated as

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{(0.5 * CF)} * a * \sigma_A \qquad (1)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \qquad (2)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,

CF : correction factor that accounts for the expected reduction in additive genetic variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),

a : random normal deviate,

σ_A : additive genetic standard deviation.

Besides the effect of inbreeding on the additive genetic variance, it is also expected to have an effect on the mean of traits subject to dominance (Falconer, 1981). The impact of both effects on response needs to be investigated. To prevent confounding of these inbreeding effects, inbreeding depression was ignored in the present paper.

Phenotypes were simulated as

$$P_i = B + A_i + e * \sigma_E \qquad (3)$$

where P_i : phenotypic value,

B : base level,

e : random normal deviate,

σ_E : environmental standard deviation.

Each week, a number of sows showed heat and a number of boars was available for mating. When no attention was paid to the additive genetic relationship of potential mates, boars mated in sequence. For maximum avoidance of mating of relatives, all combinations of potential mates, possible at the moment, were evaluated and mating was of least related animals.

2.2 Alternatives.

Sather et al. (1977) stated that avoidance of sib matings reduced inbreeding most markedly in a small population. Therefore two sizes of sow herds, 25 and 100 sows, and two numbers of boars used per year, 5 and 20, were considered. Size of the herd refers to total number of sow places available in breeding, gestation and farrowing houses. Number of boars used simultaneously was 1, 3, 5 and 10, the latter being evaluated only in case of 20 boars annually. For every alternative except use of 1 boar at a time, maximum avoidance of mating of relatives was compared to no avoidance.

2.3 Parameters

The model was applied to a sire line with characteristics as in table 1. It was assumed that 67 percent of sows that entered the breeding piggery

Table 1. General characteristics of nucleus breeding scheme.

General	
maximum number of parities per sow	5
length of suckling period (wks)	4.5
size of pool of replacement boars	4
maximum stay in pool of replacement boars (wks)	11
Performance test	
minimum start growth (0 to 23 kg, $g.day^{-1}$)	300
maximum number of boars tested per litter	2
maximum number of gilts tested per litter	6
total number of testplaces in a division	50
minimum index at end of test, boars	85
minimum index at end of test, gilts	65
percentage of boars culled for conformation	40
percentage of gilts culled for conformation	20
Sexual maturity	
percentage of boars culled for reproduction or conformation	40
percentage of gilts culled for conformation	20

farrowed. Probabilities that sows were culled at weaning for conformation or health problems were 10.0, 7.0, 7.5 and 10.0 percent for first, second, third, and fourth or greater parities. This culling was independent of the sow's performance for (re)production traits. Every week, a number of sows was selected for breeding. These sows came from the group of sows weaned in the previous week or from the pool of replacement gilts. Selection criterion was a performance index, that included production traits only.

Breeding goal (H) and selection index (I) were according to De Roo (1987a):

$$H= 0.178 * A_{GR} - 0.05 * A_{FI} + 3.0 * A_{LEAN} \tag{4}$$

$$I_{boars}= 0.0212 * P_{GR} - 0.0004 * P_{FI} + 1.5548 * P_{LEAN} \tag{5}$$

$$I_{gilts}= 0.0357 * P_{GR} - 2.5965 * P_{SF} \tag{6}$$

where A_i,P_i: breeding values and phenotypes for trait i,

GR : growth rate 23 to 100 kg (g.day^{-1}),

FI : feed intake (g.day^{-1}),

LEAN : lean percentage,

SF : side-fat thickness (mm).

Potential breeding animals were performance tested. Boars were fed ad libitum, whereas gilts were kept on a restricted diet. Only the animal's own performance data were included in the index. Variables in (5) and (6) were deviations from batch means. Index values were standardized at a mean level of 100 with a standard deviation of 32. In presentation of results, attention will be focussed on production traits in boars. Genetic and phenotypic parameters of production traits in the base population are in table 2.

Lean percentage in boars was assumed to be estimated on live animals by means of modern equipment (R^2= 0.70). Breeding values for lean percentage were assumed to be normally distributed, phenotypes were expressed on a scale with a minimum of 35 and a maximum of 75 percent (De Roo, 1987a).

Selection of young breeding animals was a multi-stage process. At the end of the test a number of animals was culled for conformation and a relative mild selection on index was performed (table 1). At sexual maturity another number of animals was culled for conformation. In addition, a number of boars was culled because of a bad reproductive performance. For each sex,

Table 2. Genetic and phenotypic parameters of production traits in the base population.

Trait	Mean	h^2	σ_p	Correlations[a]		
				GR	FI	LEAN
growth rate (GR, $g.day^{-1}$)	900	.25	88	--	.85	-.15
feed intake (FI, $g.day^{-1}$)	2 400	.25	200	.65	--	-.35
lean percentage (LEAN)	52	.45	2.5	-.10	-.30	--

[a] Upper triangle: genetic correlations, lower triangle: phenotypic correlations

the animals with the highest indices among the remaining boars or sows were ultimately selected for breeding.

2.4 Evaluation of changes in inbreeding coefficient over time and its effect on within-line additive genetic variance

Effects of mating policy on realized changes in inbreeding coefficient (F) were compared to expectations from theory of effective population size (Wright, 1931). Realized values of the yearly relative increase of the inbreeding coefficient (ΔF_r) were calculated from (Falconer, 1981):

$$\Delta F_r = (F_t - F_{t-1}) / (1 - F_{t-1}) \tag{7}$$

where F_t, F_{t-1} : average inbreeding coefficients of performance tested boars at year t and t-1.

Data of years 6 to 25 were used in the calculation of ΔF_r.

Expected yearly relative increases of F (ΔF_e) were calculated according to Hill (1972):

$$\Delta F_e = (1/ N_m + 1/ N_f) / (8 * L^2) \tag{8}$$

where L : length of generation interval,

N_m, N_f : numbers of males and females used for breeding during a year.

Inbreeding is expected to reduce within-line additive genetic variance. In a random mating population with no selection, additive genetic variance is expected to follow (Falconer, 1981):

$$V_{A_t} = (1 - F_t) * V_{A_0} \qquad (9)$$

where V_{A_t} : additive genetic variance at time t,
V_{A_0} : additive genetic variance in the base population.

Selection is expected to reduce additive genetic variance further (Bulmer, 1971; Robertson, 1977; Fimland, 1979). In a finite population, effects of selection on additive genetic variance and on response can not easily be predicted (e.g. Hill, 1977). Effects of selection on additive genetic variance were evaluated by comparing realized reductions of within-line additive variance with expectations for a situation of random mating and no selection. To make these effects as clear as possible, expected reductions were based on realized values of F.

3. RESULTS AND DISCUSSION

3.1 Characteristics of the herd

Characteristics of sows were similar to values reported for sow herds of the same size by De Roo (1987b) and are not presented. Characteristics of breeding boars are in table 3. Number of boars used per year was in agreement with the desired number except in case of 25 sows and 20 boars annually. In this situation replacement boars were not always available, which led to a slightly less than desired annual number of boars. As a result, mean and standard deviation of number of weeks boars were used for breeding were higher for alternatives with 25 sows and 20 boars annually compared to 100 sows and 20 boars. Boars were replaced at regular time intervals to secure regular selection of new boars (De Roo, 1987b). As a result, standard deviation of number of weeks in service was low.

For alternatives with avoidance of mating of relatives, the variation in number of matings per boar was larger than for the comparable alternative without avoidance of mating of relatives. For the latter alternatives, standard deviations of number of matings per boar decreased when number of boars used simultaneously increased because random deviations in number of

Table 3. Characteristics of breeding boars.

Alternative[a]	Matings per boar mean	Matings per boar sd	Weeks in service mean	Weeks in service sd	Age at culling (yr)
25 5 1 -	14.3	2.7	10.4	.6	.97
25 5 3 +	14.4	7.1	31.1	.5	1.37
25 5 3 -	14.2	1.3	31.1	.5	1.37
25 5 5 +	14.3	10.6	51.8	.1	1.76
25 5 5 -	14.3	.8	51.7	.1	1.76
25 20 1 -	3.9	2.2	2.8	1.1	.78
25 20 3 +	3.8	2.6	8.3	1.6	.87
25 20 3 -	3.8	1.2	8.4	1.7	.88
25 20 5 +	3.8	2.9	13.6	1.9	.97
25 20 5 -	3.8	.9	13.8	2.0	.97
25 20 10 +	3.7	3.6	26.8	2.4	1.22
25 20 10 -	3.7	.6	26.7	2.3	1.22
100 5 1 -	56.2	5.8	10.4	.6	.97
100 5 3 +	55.7	14.4	31.2	.5	1.37
100 5 3 -	56.3	2.4	31.2	.5	1.37
100 5 5 +	56.0	39.6	52.0	.0	1.77
100 5 5 -	55.6	1.3	52.0	.0	1.76
100 20 1 -	13.9	4.0	2.6	.5	.78
100 20 3 +	13.9	6.2	7.8	.4	.88
100 20 3 -	14.0	1.7	7.8	.4	.88
100 20 5 +	14.0	7.8	13.0	.0	.98
100 20 5 -	14.0	1.2	13.0	.0	.98
100 20 10 +	14.0	12.0	26.0	.0	1.23
100 20 10 -	14.1	.7	26.0	.0	1.23

[a] Alternatives are characterized as size of the sow herd, annual number of boars, number of boars used simultaneously and avoidance (+) or no avoidance (-) of mating of relatives.

sows in heat were more evenly distributed over boars. For alternatives with avoidance of mating of relatives, the opposite was observed: the larger the number of boars in service, the larger the variation in number of matings per boar. At a fixed annual number of boars, an increase in number of boars used simultaneously corresponds to an increase in number of weeks in service. The time in which differences in number of matings per boar could accumulate was, therefore, longer when number of boars used simultaneously increased.

3.2 Selection response

Overall response is expressed in Dfl. using economic weights from eq. 4. Response curves are in figure 1 and cumulative responses up to year 25 are in table 4. For alternatives with 20 boars annually and 5 boars simultaneously, only cumulative responses up to year 25 are given.

Within each combination of number of sows and annual number of boars, cumulative response was highest for alternatives with 3 boars used simultaneously (table 4). When number of boars used simultaneously increased, age of boars at culling increased (table 3) and response decreased (table 4).

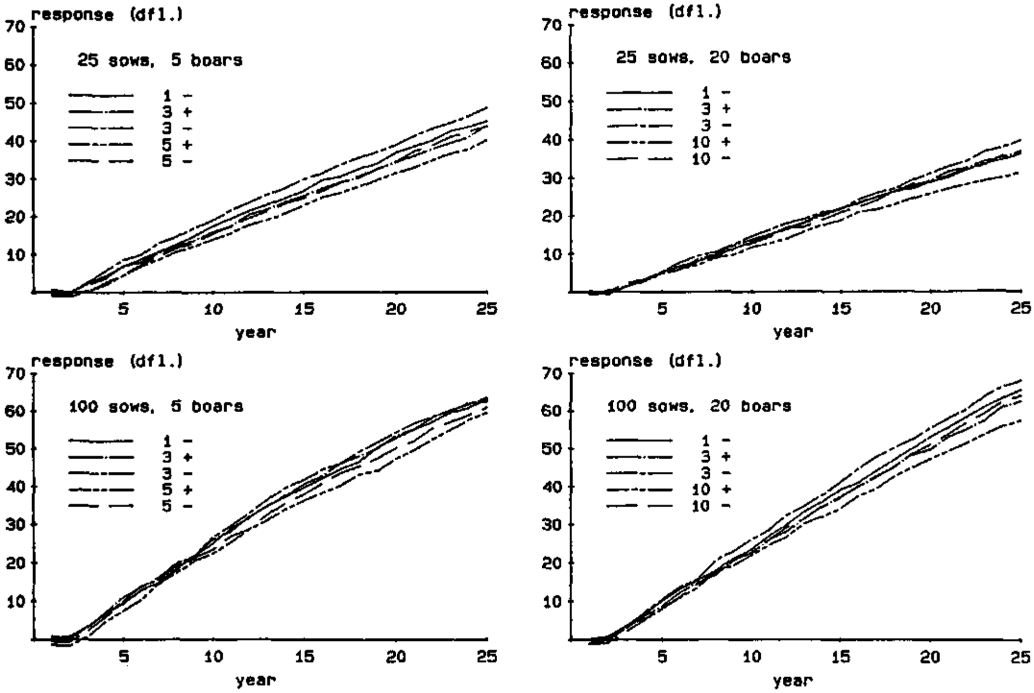

Figure 1. Mean cumulative response at different mating policies, for different population sizes. Alternatives are characterized as number of boars used simultaneously and avoidance (+) or no avoidance (-) of mating of relatives.

Table 4. Mean cumulative response up to year 25 (R_{cum}, in Dfl.), standard error of R_{cum} (sem_R), mean inbreeding coefficient (F) in year 25, between (sdb_F) and average within (sdw_F) replicate standard deviation of F, expected (ΔF_e) and realized (ΔF_r) yearly relative increase of F[a] and expected (RV_e) and realized (RV_r) reductions in additive genetic variance in year 24 (in percent).

Alternative[b]	R_{cum}	sem_R	F	sdb_F	sdw_F	ΔF_e	ΔF_r	RV_e	RV_r
25 5 1 -	44.89	1.12	34.3	2.3	4.7	1.82	1.67	33.4	39.9
25 5 3 +	43.60	1.13	28.5	1.2	1.4	1.56	1.50	27.2	38.1
25 5 3 -	48.34	1.21	34.1	2.2	4.2	1.56	1.69	33.0	36.8
25 5 5 +	39.86	.98	27.2	1.2	.9	1.37	1.47	26.2	37.5
25 5 5 -	43.53	1.05	31.3	1.9	4.1	1.37	1.55	30.0	35.6
25 20 1 -	36.22	.84	24.7	1.7	7.9	.72	1.03	23.6	22.1
25 20 3 +	36.90	1.16	17.2	.8	2.1	.69	.85	16.2	22.1
25 20 3 -	39.69	.96	21.0	2.0	5.7	.69	.93	20.1	21.8
25 20 5 +	33.56	1.10	15.9	.6	.9	.66	.82	15.2	23.7
25 20 5 -	38.42	.85	19.3	1.7	4.4	.66	.87	18.7	21.6
25 20 10 +	31.28	1.02	14.7	1.1	.5	.60	.78	14.0	24.5
25 20 10 -	36.34	1.11	16.7	1.4	4.1	.59	.76	16.0	19.1
100 5 1 -	63.11	2.25	29.9	1.5	4.2	1.59	1.41	29.1	30.5
100 5 3 +	63.64	1.93	25.2	1.4	1.2	1.37	1.32	24.2	36.0
100 5 3 -	62.63	1.92	32.1	2.7	3.7	1.37	1.62	31.6	36.3
100 5 5 +	59.49	2.48	23.7	.9	.9	1.19	1.27	22.5	31.1
100 5 5 -	60.91	1.87	28.1	3.6	3.6	1.19	1.35	27.3	30.5
100 20 1 -	65.53	1.87	15.8	1.7	6.0	.49	.63	14.5	12.6
100 20 3 +	62.48	1.27	10.6	.6	1.4	.46	.52	10.1	17.5
100 20 3 -	67.94	1.50	13.8	.5	4.3	.46	.58	13.4	9.7
100 20 5 +	62.53	.99	10.0	.4	.7	.45	.51	9.5	13.8
100 20 5 -	65.23	1.15	13.3	.1	3.9	.45	.58	12.6	16.8
100 20 10 +	57.30	1.46	10.1	.4	.4	.41	.53	9.6	17.3
100 20 10 -	64.03	1.38	12.2	.4	3.3	.41	.55	11.6	15.0

[a] Averages over years 6 to 25

[b] Alternatives are characterized as size of the sow herd, annual number of boars, number of boars used simultaneously and avoidance (+) or no avoidance (-) of mating of relatives.

Increasing number of boars used simultaneously from 3 to 5 or from 5 to 10 did not increase additive genetic variance enough to compensate for lengthening of the generation interval.

Responses with 1 boar at a time were only slightly less than those with 3 boars used simultaneously. This indicates that within-family selection might yield good results, in agreement with Demple (1975). Further investigations of this selection system are justified.

Despite considerably lower levels of the inbreeding coefficient for alternatives with avoidance of mating of relatives (table 4), which is expected to keep the usable additive genetic variance at higher levels (eq. 9), responses were lower than for alternatives without avoiding mating of relatives. Avoiding mating of relatives led to marked differences in number of matings per boar (table 3). It is likely that, because selection was on phenotype alone, sires with few relatives were not as good genetically, on average, as sires with many relatives. The differential usage of sires with few relatives, thus, contributed to reduced selection response. Moreover, the usable additive genetic variance was lowest when mating of relatives was avoided (table 4), contrary to expectations.

Expected and realized reductions in within-line additive genetic variance are in table 4. Expectations were calculated for a situation of random mating, ignoring selection. As indicated by De Roo (1987b), selection caused a considerable reduction of the additive genetic variance. These reductions were in general largest for alternatives with avoidance of mating of relatives. With this mating system, breeding values of mates, on average, will be more diverse than without avoidance of mating of relatives, where some matings might be inbred. Avoidance of mating of relatives, thus, is expected to lead to a reduction in additive genetic variance among offspring relative to no avoidance. In addition, unequal contributions of sires to the next generation of offspring will have reduced the usable additive genetic variance in the case of avoidance of mating of relatives.

The difference in cumulative response in year 25 between alternatives with and without avoidance of mating of relatives was clear except for alternatives with 100 sows and 5 boars annually. For these alternatives, selection was intense and number of sires that contributed to the pool from which new breeding animals were selected was small. Sires with a high breeding value will have more offspring selected for breeding when selection is intense. This means a continuous reduction in effective number of sires over time. As a result, between-sire variance and selection intensity are reduced over time. This reduction is most serious when annual number of boars is small (Hill, 1976, 1977; De Roo, 1987b). Avoidance of mating of relatives favoured sires with few relatives and, thus, limited the reduction of the effective number of sires. Differences in response between alternatives with and without avoidance of mating of relatives, therefore, were small. Other alternatives did not show a similar trend because selection was less intense (25 sows) or because annual number of boars was sufficiently large (20 boars annually).

3.3 Inbreeding coefficient

Changes in inbreeding coefficient (F) over time are in figure 2. Avoiding mating of relatives initially postponed the increase of F, but changes in F after year 5 were rather independent of the mating policy. Within each combination of number of sows, annual number of boars and number of boars

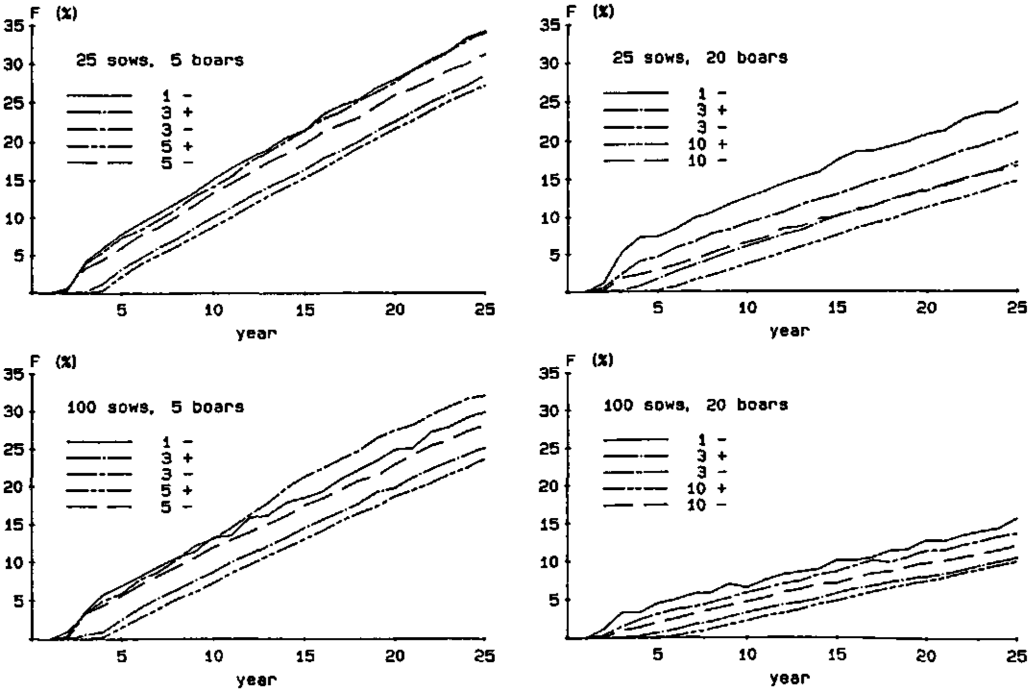

Figure 2. Mean inbreeding coefficient at different mating policies, for different population sizes. Alternatives are characterized as number of boars used simultaneously and avoidance (+) or no avoidance (-) of mating of relatives.

used simultaneously, realized values of the yearly relative increase of F (ΔF_r) for both mating policies were close. Avoiding mating of relatives could, thus, only postpone but not prevent the increase in F. This is reasonable because possibilities of finding unrelated mates decreased with time. Compared to random mating, avoidance of mating of relatives leads to a population of more equally related individuals. This is illustrated by the small within-line standard deviation of F for these alternatives (table 4). The advantage of avoiding mating of relatives with respect to ΔF_r compared to random mating gradually diminish and will, after many generations, turn into a disadvantage (Robertson, 1964).

As with selection response, alternatives with 100 sows and 5 boars annually provided different results. Contrary to the situation of 25 sows, 5 boars annually and 3 boars simultaneously, for example, the difference in ΔF_r with and without avoiding mating of relatives was relatively large for 100 sows, 5 boars annually and 3 boars simultaneously. With intense selection and few boars annually more offspring of sires with a high breeding value were selected, which increased F and decreased cumulative response (figure 2, table 4). Avoidance of mating of relatives favoured usage of sires with few relatives. Breeding values of these sires probably were less than those of sires with many relatives, which means that the effect of selection on F was lower with this mating policy.

Despite similarities in increase in F after year five, there were considerable differences in F in year 25 between alternatives with and without avoidance of mating of relatives (table 4). A mating policy that ignored the additive genetic relationship of mates not only had a higher average level of F, but also resulted in larger between-line standard deviations of F. The risk of an unexpected high level of F, therefore, is higher when there is no avoidance of mating of relatives.

An increase in number of boars used simultaneously caused a decrease in differences between alternatives with and without mating of relatives. This is because of the inequality in number of matings per boar (table 3). When number of boars used simultaneously increased, standard deviation of number of matings per boar decreased for alternatives without avoidance of mating of relatives and increased for alternatives with avoidance of mating of relatives. A more equal distribution of family size has a positive effect on effective population size (Hill, 1972) and results in a slower increase of F. Increase of the number of boars used simultaneously, therefore, had a positive effect on effective population size for alternatives without avoidance of mating of relatives, but a smaller or even negative effect for alternatives in which the mating of relatives was avoided.

The detrimental effect of unequal family size is illustrated clearly when expected (ΔF_e) and realized (ΔF_r) yearly relative increases of F are compared (table 4). When number of boars used simultaneously increased, a decline in ΔF was expected, because of lengthening of the generation interval (eq. 8). The realized decline in ΔF was smaller than expected or even absent for alternatives with avoidance of mating of relatives (compare alternatives 100 20 5 + to 100 20 10 +). The decline in ΔF_r for alternatives without avoidance of mating of relatives was always larger than for alternatives with avoidance.

Comparison of expected and realized values of ΔF indicates that selection caused ΔF_r to be larger than ΔF_e (table 4), in agreement with Robertson (1961) and Belonsky and Kennedy (1987). De Roo (1987b) found that avoidance of sib mating could counteract the effect of selection. Realized and expected values of ΔF were generally close. Extra benefits with respect to ΔF could be expected from maximum avoidance of mating of relatives. The unequal distribution of family size, however, caused ΔF_r to be in general larger than ΔF_e.

Despite a shorter generation interval, ΔF_r for alternatives with 5 boars annually and 1 boar at a time was less than for similar alternatives with 3 boars at a time. The former alternative tends to within-family selection, which is expected to reduce the rate of increase in F (Hill, 1972). The short generation interval caused F to be high relative to alternatives with avoidance of mating of relatives. For alternatives with 20 boars annually and 1 boar at a time, ΔF_r was not smaller than for alternatives with 3 boars at a time because more sires contributed to the young boar pool from which new breeding stock were selected than for alternatives with 5 boars annually. This was possibale because the permitted stay of young boars in the pool was 11 weeks for all alternatives (table 1).

3.4 General discussion

Rendel and Robertson (1950) showed the favourable effect of a short generation interval on selection response. A short generation interval, however, is unfavourable with respect to the rate of increase in F (Hill, 1972). Lenghtening of the generation interval, by means of increasing number of boars used simultaneously reduced F (table 4). This did not increase the additive genetic variance available for selection enough to compensate the negative effect of a longer generation interval on selection response. Compared to use of 1, 5 or 10 boars simultaneously, use of 3 boars at a time was optimal.

Similarities in rate of increase in F after year 5 between alternatives with and without avoidance of mating of relatives (table 4, figure 2), do not mean that the mating strategy does not influence the rate of increase in F in later years. Effects of a change in allowed degree of additive genetic relationship of mates for the situation of 100 sows, 20 boars annually and 3 boars simultaneously, are in table 5. A change of the mating strategy after year 5 from maximum avoidance to no avoidance of mating of relatives caused the loss of the initial advantage in level of F. In case of continued random mating, accidently unrelated individuals will be mated, which compensates for the unintentional mating of, for example, full sibs. This possibility does not exist anymore after several generations of avoidance of mating of relatives. This explains how a change of mating policy from avoidance to no avoidance of mating of relatives led to a fast increase of F. A change of mating strategy is, thus, not advisable. It is also clear from table 5 that maximum avoidance of mating of relatives has only a slight advantage relative to the more simple system of avoidance of half sib mating.

Table 5. Mean cumulative response (R_{cum}) and inbreeding coefficient (F) in year 25 at different maximum allowed additive genetic relationships of mates (F_{max})[a], for the situation of 100 sows, 20 boars annually and 3 boars simultaneously.

F_{max} in year		R_{cum}	F
1 - 5	6 - 25		
0.0	0.0	62.48	10.6
12.5	12.5	65.92	11.4
99.9	99.9	67.94	13.8
0.0	12.5	64.48	11.0
0.0	25.0	64.56	12.6
0.0	99.9	65.34	13.9

[a] F_{max} is 0.0 means maximum avoidance and F_{max} is 99.9 means no avoidance of mating of relatives.

A strategy of splitting the population into sublines and keep these lines as independent breeding groups, might be useful with respect to limiting the rate of increase in F (Robertson, 1964). Splitting of a line into isolated sublines, however, causes considerable loss of selection response (De Roo, 1987b) and is, therefore, unadvisable in pig nucleus breeding. Circular mating systems (De Rochambeau and Chevalet, 1982) which combine within-family selection and avoidance of mating of relatives, might be useful in pig breeding, especially when family size is large and accuracy of index selection is high (Dempfle, 1975). The comparison of mass selection and within-family selection needs further investigation. The benefits of mating systems that limit the rate of increase in F increase if there is inbreeding depression. This simulation was under an additive genetic model and inbreeding depression was not a consideration.

Results from table 4 and from De Roo (1987b) showed that use of more than 5 boars annually is favourable with respect to selection response when size of the sow herd is larger than 25. Increases in annual number of boars reduced the rate of increase in F and kept additive genetic variance available for selection at a higher level. A further reduction of the rate of increase in F can be obtained from avoiding mating of relatives. Such a system will be beneficial when it is applied with the restriction of equal family size.

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Chapter 5

STUDIES ON BREEDING SCHEMES IN A CLOSED PIG POPULATION

3. Founder effects

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ABSTRACT

A stochastic model was used to examine founder effects on selection response and inbreeding coefficient in a closed swine herd. Effects of changes in size of the founder population, in effective population size after the foundation period and in intensity of selection of founder animals from a base population were evaluated.

Determination of optimal size of the founder population implies a balancing of mean breeding value and additive genetic variance in the founder group. Optimal number of founder animals depends on differences in estimated breeding values between animals, on the accuracy of these estimates and on the risk of low response a breeder is willing to take. This risk increases at a decreasing number of founder animals.

Use of five founder boars provided, on average, good responses. The established level of additive genetic variance offered good possibilities for further selection and fast reduction of this variance in the early years of the breeding program was prevented.

Optimal number of founder sows depended on desired size of the herd. A gradual increase of number of sows towards the desired size of the herd was optimal. This strategy implies culling of sows with a low performance, even if the desired size of the herd is not reached yet. Selection of sows should be mild, because build up of the herd should be done fast. A herd of 100 sows could be founded acceptably by 25 founder sows.

A temporary restriction of population size did not diminish responses as long as it was not too severe. An increase of effective population size after such a bottleneck affected response and rate of increase in the inbreeding coefficient.

1. INTRODUCTION

When starting a new line in pig nucleus breeding, the question of size of the founder population arises. The founder population should have a high mean breeding value and contain a substantial amount of genetic variation to allow further improvement by selection (James, 1984). These requirements, however, conflict. Selection of founder animals decreases genetic variance available for further selection (Bulmer, 1971, 1976). Moreover, a small effective population size reduces genetic variance because of random loss of genes (Falconer, 1981). The initial advantage of a small, highly selected founder population might, thus, be offset by reduced possibilities for further selection in later generations.

Robertson (1960) concluded that temporary restriction of population size reduced the selection limit dramatically. Continued restriction of population size would have small additional effects because frequency of desired genes would be at a higher level which reduces the probability of random loss of a gene (Kimura, 1957). James (1971) studied founder effects for a single locus with additive gene action. He stated that Robertson's theory should not be interpreted as suggesting that after an initial bottleneck, subsequent selection may be done safely with small numbers. When few animals are selected for breeding, there is still a probability that favorable genes are lost by chance.

James' study considered a single locus situation, whereas production traits in pig breeding are assumed to be influenced by many loci. Also, pig breeders are more interested in response over the first 10 to 20 generations of selection, than in the limit situation described by Robertson (1960) and James (1971, 1984).

Determination of optimal size of the founder population for the practical situation of a pig nucleus is complicated (James, 1971). The aim of this paper was to study effects of different sizes of founder population on selection response and inbreeding coefficient over time. Effects of intensity of selection of founder animals from a base population and effects of increasing effective population size after the foundation period were also considered. A model of a closed pig population (De Roo, 1987a) was used.

2. MATERIAL AND METHODS

2.1 Model

The model described by De Roo (1987a,b) measured changes in production and reproduction traits and inbreeding coefficient over 25 years of selection in a closed swine herd. Growth rate (23 to 100 kg), feed intake, lean percentage, litter size and interval from weaning to oestrus were incorporated in the model because of their economic relevance to pig breeders. The model included overlapping generations, continuous mating and farrowing and weekly selection of boars and sows. Week was the unit of time.

De Roo (1988) argued that an infinitesimal model, in which traits are affected by an infinite number of unlinked loci of small effect each, would provide useful information to pig breeding. An additive, infinitesimal model was used in this paper, epistatic effects were ignored. Breeding values were generated as

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{(0.5 * CF)} * a * \sigma_A \qquad (1)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \qquad (2)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,

CF : correction factor that accounts for the expected reduction in additive genetic variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),

a : random normal deviate,

σ_A : additive genetic standard deviation.

Besides the effect of inbreeding on the additive genetic variance, it is also expected to have an effect on the mean of traits subject to dominance (Falconer, 1981). The impact of both effects on response needs to be investigated. To prevent confounding of these inbreeding effects, inbreeding depression was ignored in the present paper.

Phenotypes were simulated as

$$P_i = B + A_i + e * \sigma_E \qquad (3)$$

where P_i : phenotypic value,

B : base level,

e : random normal deviate,

σ_E : environmental standard deviation.

Introduction of founder sows in the herd at about 8 months of age (De Roo, 1987a) was evenly spread over the first half year of the breeding program to prevent large fluctuations in number of offspring available for selection and, thus, in selection intensity in the first years of selection. All founder boars were available simultaneously for breeding and mated sequentially. This method minimized differences in number of matings per founder boar because it was not affected by random fluctuations in number of sows that showed heat.

2.2 Alternatives

Effects of founder population size, intensity of selection of founder animals from a base population and of population size after the foundation period were studied separately except when a combination of effects seemed important.

Founder animals were selected from a base population. Number of founder sows refers to number of sows expected to farrow at least once. Because of fertility problems not all sows that were introduced in the herd farrowed. With parameters described by De Roo (1987a), number of sows to be selected from the base population was 1.5 times number of founder sows. This was taken into account when selection intensities were considered. For example an alternative with 25 founder sows and 75 base sows meant that 38 sows would be selected from the base population, the proportion selected, thus, was 50 percent. Size of the sow herd refers to total number of sow places available in breeding, gestation and farrowing houses. All base boars were assumed to be fertile and capable of mating.

The alternative with 25 founder sows selected from 75 base sows, 5 founder boars selected from 30 base boars and a herd size of 100 sows and 15 boars annually served as a reference. Alternatives differed from the reference situation only with respect to one or two parameters. These alternatives were:

- Size of founder sow population.
  Number of founder sows was 15, 25 and 50. For each, increase of the sow herd after the foundation period to 50 or 100 sows was considered. Number of base sows was 75 for all alternatives.
- Intensity of selection of founder sows from a base population.
  At a constant number of founder sows (25), number of base sows was varied from 38, 75, 150 to 225.
- Size of the founder boar population.
  Number of founder boars varied from 1, 3, 5, 10 to 15.
- Intensity of selection of founder boars from a base population.
  Size of the base boar population varied from 15, 30, 60 to 90. For each, results with 1, 5 and 15 founder boars were considered.
- Annual number of boars.
  Effects of increasing effective population size after the foundation period were studied by means of increasing annual number of boars from 5, 10 to 15. Number of founder boars was 5 for all alternatives. Optimal

annual number of boars depends on size of the sow herd (De Roo, 1987b). Therefore, two sizes of the sow herd were considered, 50 and 100.

Three boars were used simultaneously for breeding after the foundation period. Mating of relatives was avoided; maximum inbreeding coefficient of potential offspring was 0.125. If no potential mates met this requirement, least related individuals were mated. Because size of the founder population was small, 20 replicates were done for all alternatives.

2.3 Parameters

The model was applied to a sire line with characteristics as in table 1. It was assumed that 67 percent of sows that entered the breeding piggery farrowed. Probabilities that sows were culled at weaning for conformation or health problems were 10.0, 7.0, 7.5 and 10.0 percent for first, second, third, and fourth or greater parities. This culling was independent of the sow's performance for (re)production traits. Every week, a number of sows was selected for breeding. These sows came from the group of sows weaned in the previous week or from the pool of replacement gilts. Selection criterion was a performance index, that included production traits only.

Breeding goal (H) and selection index (I) were according to De Roo (1987a):

$$H= 0.178 * A_{GR} - 0.05 * A_{FI} + 3.0 * A_{LEAN} \quad (4)$$

$$I_{boars}= 0.0212 * P_{GR} - 0.0004 * P_{FI} + 1.5548 * P_{LEAN} \quad (5)$$

$$I_{gilts}= 0.0357 * P_{GR} - 2.5965 * P_{SF} \quad (6)$$

where A_i,P_i: breeding values and phenotypes for trait i,
GR : growth rate 23 to 100 kg (g.day^{-1}),
FI : feed intake (g.day^{-1}),
LEAN : lean percentage,
SF : side-fat thickness (mm).

Potential breeding animals were performance tested. Boars were fed ad libitum, whereas gilts were kept on a restricted diet. Only the animal's own performance data were included in the index. Variables in (5) and (6) were deviations from batch means. Index values were standardized at a mean level

Table 1. *General characteristics of nucleus breeding scheme.*

General	
maximum number of parities per sow	5
length of suckling period (wks)	4.5
number of boars used simultaneously	3
size of pool of replacement boars	4
maximum stay in pool of replacement boars (wks)	11
maximum additive genetic relationship of mates	0.125
Performance test	
minimum litter size at weaning	6
minimum start growth (0-23 kg, $g.day^{-1}$)	300
maximum number of boars tested per litter	2
maximum number of gilts tested per litter	6
total number of testplaces in a division	50
minimum index at end of test, boars	85
minimum index at end of test, gilts	65
percentage of boars culled for conformation	40
percentage of gilts culled for conformation	20
Sexual maturity	
percentage of boars culled for reproduction or conformation	40
percentage of gilts culled for conformation	20

of 100 with a standard deviation of 32. In presentation of results, attention will be focussed on production traits in boars. Genetic and phenotypic parameters of production traits in the base population are in table 2.

Lean percentage in boars was assumed to be estimated on live animals by means of modern equipment ($R^2 = 0.70$). Breeding values for lean percentage were assumed to be normally distributed, phenotypes were expressed on a scale with a minimum of 35 and a maximum of 75 percent (De Roo, 1987a).

Selection of young breeding animals was a multi-stage process. At the end of the test a number of animals was culled for conformation and a relative mild selection on index was performed (table 1). At sexual maturity another number of animals was culled for conformation. In addition, a number of boars was culled because of a bad reproductive performance. For each sex,

Table 2. Genetic and phenotypic parameters of production traits in the base population.

Trait	Mean	h^2	σ_p	Correlations[a] GR	FI	LEAN
growth rate (GR, $g.day^{-1}$)	900	.25	88	--	.85	-.15
feed intake (FI, $g.day^{-1}$)	2 400	.25	200	.65	--	-.35
lean percentage (LEAN)	52	.45	2.5	-.10	-.30	--

[a] Upper triangle: genetic correlations, lower triangle: phenotypic correlations

the animals with the highest indices among the remaining boars or sows were ultimately selected for breeding.

2.4 Evaluation of changes in the inbreeding coefficient (F) over time

The yearly relative increase of the inbreeding coefficient (ΔF_r) is a convenient measure of the rate of inbreeding (Falconer, 1981). Whereas the absolute yearly increase of F will diminish as homozygosity is increased, ΔF_r will be constant unless effective population size changes. ΔF_r was calculated from

$$\Delta F_r = (F_t - F_{t-1}) / (1 - F_{t-1}) \qquad (7)$$

where F_t, F_{t-1} : inbreeding coefficient at year t and t-1.
Values of F were used to compare effects of different breeding schemes on rate of inbreeding.

3. RESULTS AND DISCUSSION

3.1 Size of founder sow population

Number of founder sows determined the time period required until the sow herd reached its desired size (table 3). With 15 founder sows it took five to six years to build up a sow herd of 100 sows. It took four to five years with 25 founder sows and three to four years with 50 founder sows.

Table 3. Average number of sows in the herd in the first years of the breeding program as a function of number of founder sows and desired size of the herd.

No. of founder sows	Desired herd size	Average number of sows in year				
		1	2	3	4	5
15	50	10.1	22.0	38.1	47.7	49.9
25	50	16.4	32.0	46.4	49.4	50.5
50	50	33.4	45.6	49.8	50.1	50.6
15	100	9.8	19.2	38.7	73.9	96.1
25	100	16.1	33.6	65.3	94.8	100.4
50	100	32.4	65.6	95.6	100.1	100.7

A sow herd of 50 sows was build up about one year faster than a sow herd of 100 sows for the same number of founder sows. Culling levels for fertility and conformation influenced the time required to build up a sow herd. Lower culling levels would have reduced time lag and differences in time lag between alternative number of founder sows.

Overall response is expressed in Dfl. using economic weights from eq. 4. Use of 15 founder sows gave an advantage in response in years two and three (figure 1). A higher number of founder sows, however, resulted in more litters in the early years of the breeding program, which increased possibilities for selection. This offset the initial advantage of starting with a smaller, more strongly selected number of founder sows.

In the case of 100 sows, the alternative with 50 founder sows was superior to alternatives with fewer founder sows from year three on (figure 1). The difference in cumulative response in year 25 between alternatives with 50 and 25 founder sows, however, was small (table 4). In the case of 50 sows, 25 founder sows gave best results, differences with other alternatives were small (figure 1).

Optimum number of founder sows depended on desired size of the sow herd because the time required to establish a herd depended on herd size and number of founder sows. The faster the build up of a herd, the sooner advantage could be taken of available test capacity. The time lag between alternatives with 25 and 50 founder sows was short for a herd of 50 sows

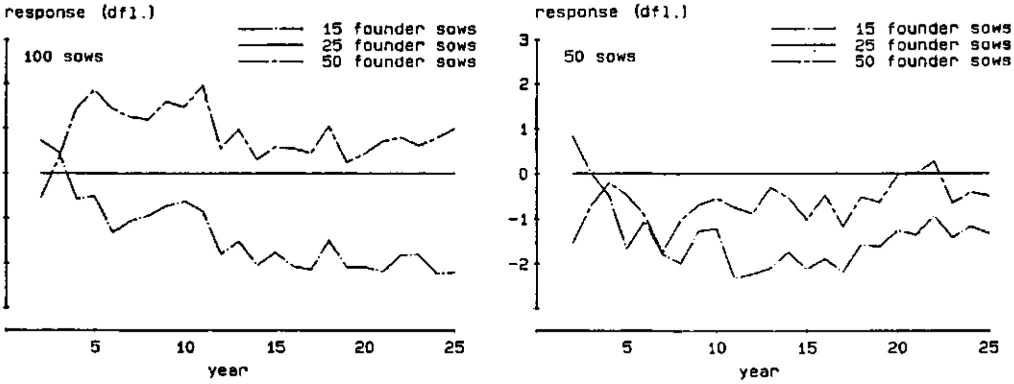

Figure 1. Cumulative response over time as a function of number of founder sows, for two sizes of the sow herd. Responses are deviations from cumulative response with 25 founder sows.

Table 4. Cumulative response (R_{cum}), inbreeding coefficient (F) and their standard errors (sem_R and sem_F) in year 25 and rate of increase of F (ΔF) as a function of number of founder sows and desired size of the sow herd.

No. of founder sows	Desired herd size	R_{cum}	sem_R	F	sem_F	ΔF in year	
						1-5	6-25
15	50	56.52	.93	17.1	.27	1.30	.67
25	50	57.85	.96	16.5	.16	1.09	.68
50	50	57.35	.97	16.2	.20	1.01	.68
15	100	63.79	.94	16.0	.18	1.30	.61
25	100	65.98	.72	14.7	.16	1.09	.57
50	100	66.98	.85	14.7	.13	.94	.60

relative to a herd of 100 sows. This longer time lag offset the advantage of a stronger selection among base sows for alternatives with 25 founder sows in a herd of 100 sows, but did not in a herd of 50 sows.

Within each size of the sow herd, differences in F in year 25 between alternatives were only small (table 4) and were accumulated in the first years of the breeding program: values of ΔF_r from year 6 to 25 were similar for all numbers of founder sows. This was to be expected, because after the foundation period, number of boars used annually was the same for all alternatives.

3.2 Increase of the sow herd to 50 or 100 sows

With a given number of founder sows, herds of different sizes can be established. Response curves are given for herd sizes of 50 and 100 sows for each number of founder sows considered (figure 2). With 15 or 25 founder sows, results for a herd of 50 sows were initially better than for 100 sows. Number of animals available for selection were initially similar for both herd sizes. With 50 sows, however, fewer sows were required for replacement and possibilities of selection, thus, were larger (table 5). For a sow herd of 100 sows, it took eight to nine years to catch up with a herd of 50 sows. After year ten differences in response between both sizes of the sow herd increased rapidly in favor of 100 sows.

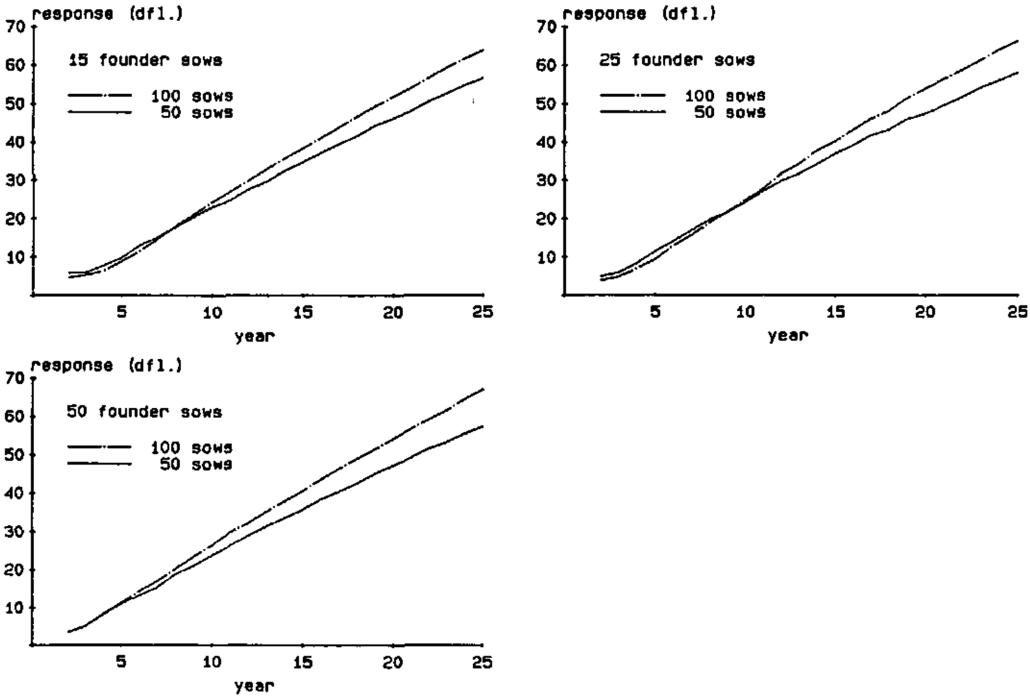

Figure 2. Cumulative response over time as a function of size of the sow herd, for three numbers of founder sows.

Table 5. Number of sows culled per year in the first years of the breeding program as a function of number of founder sows and desired size of the herd.

No. of founder sows	Desired herd size	Number of sows culled in year				
		1	2	3	4	5
15	50	6.7	13.2	38.7	61.2	68.5
25	50	10.2	25.4	56.5	64.6	66.6
50	50	20.1	54.2	66.9	66.4	66.5
15	100	6.9	11.7	27.2	66.6	124.9
25	100	10.1	20.3	53.2	114.9	135.5
50	100	21.5	44.1	116.8	130.3	125.8

With 50 founder sows, a herd size of 100 sows was superior from the start of the breeding program (figure 2). In the case of 100 sows and 50 founder sows number of litters produced per year and, thus, test capacity used, increased rapidly. Number of animals available for selection, therefore, was larger than with 50 sows and despite the higher number of sows required for replacement with 100 sows, response was better than with 50 sows.

Similar response in the first ten years of the breeding program can be obtained at lower costs with a smaller sow herd. In the long term, however, a larger herd is beneficial (figure 1, table 4), in agreement with De Roo (1987b). To obtain these extra benefits, extra investments in the early years of selection are necessary. The alternative of delaying the increase of size of the herd to, for example, year ten would mean that the response curve would fall below or at least follow the curve for 50 sows (figure 2) for a couple of years and would, thus, generate a considerable time lag relative to an immediate increase of size of the herd to 100 sows. A delay of the increase of the herd to year five or year six might be a compromise to reduce costs without reduction of benefits. At that time, the response curve for 50 sows is still above the curve for 100 sows, which makes a little loss due to a temporary low selection in sows acceptable. Moreover, increase of the sow herd and of test capacity used, can be fast when a herd of 50 sows is available.

3.3 Effects of different selection intensities in selecting founder sows from a base population

Alternatives with a different number of base sows, but with the same number of founder sows (25) were considered. Expected response to selection among base sows (R_e) was calculated from selection index theory:

$$R_e = 0.5 * i * \sigma_I \tag{8}$$

where i : standardized selection intensity,

σ_I : standard deviation of index.

Selection intensities were from tables for selection from finite numbers (Becker, 1975); σ_I was Dfl. 2.65, the value that corresponded to selection of gilts (eq. 6).

Values of R_e were Dfl. 1.03, 1.66 and 1.97 for 75, 150 and 225 base sows, respectively. Realized changes in response because of selection among base sows are in figure 3. This selection was, in general, beneficial. A higher selection intensity, however, was no guarantee of a higher response because results for replicate lines differed considerably as a result of drift. Standard error of the mean over replicates in year 25 was 0.72, on average, which is large compared to differences in R_e. Results in year one were relatively unreliable because they were based on data of few animals: the test capacity was hardly used in year one. Response to selection among

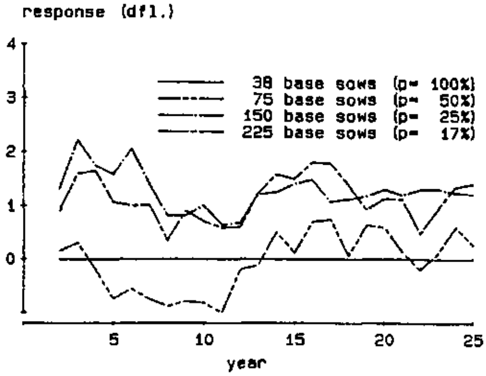

Figure 3. Cumulative response over time as a function of size of the base sow population. Responses are deviations from cumulative response with 38 base sows; p is the fraction of base sows selected for breeding.

base sows, averaged over years 2 to 25, were Dfl. -0.05, 1.25 and 1.10 for 75, 150 and 225 base sows, which was considerably less than suggested by R_e.

Comparison of expected and realized response to selection among base sows is complicated by the relative large variation in response between replicate lines. Response for the control alternative with random selection among base sows could, by chance, be overestimated which would cause underestimation of differences of expected and realized response. A systematic influence on response, however, was expected from selection (Bulmer, 1971, 1976). Because of selection among base sows, the between-dam variance component in offspring of founder sows was reduced relative to no selection. This reduction was larger when selection was more intense (Bulmer, 1971; Robertson, 1977; Fimland, 1979). Prospects of further selection, thus, were highest when the preceding selection pressure was lowest. The initial advantage of intense selection among base sows, thus, were offset partly by the reduced additive genetic variance that accompanied this intense selection.

3.4 Size of founder boar population

Size of founder boar population selected from 30 base boars available varied from 1 to 15. Results are in table 6.

Cumulative response up to year 25 was highest for the alternative with five founder boars. Use of a smaller number of founder boars showed poorer

Table 6. Cumulative response (R_{cum}), inbreeding coefficient (F) and their standard errors (sem_R, sem_F) in year 25 and rate of increase of F (ΔF) as a function of number of founder boars.

No. of founder boars	R_{cum}	sem_R	F	sem_F	ΔF in year	
					1-5	6-25
1	61.62	1.03	21.7	.25	3.02	.60
3	63.74	.85	16.3	.16	1.45	.59
5	65.98	.72	14.7	.16	1.09	.57
10	64.97	.68	14.0	.09	.78	.59
15	64.52	.47	13.4	.16	.76	.57

responses, but differences with a higher number of founder boars were relatively small. Standard errors of means over replicates (sem_R) differed considerably (table 6). Results for each alternative were based on 20 replicates, which means that standard deviation of replicate means was $\text{sem}_R*\sqrt{20}$. Differences in response between replicates were high when number of founder boars was small and decreased when number of founder boars increased. Use of less than five founder boars, thus, not only resulted in a lower average response over replicates, but also in a higher risk of low response for individual replicates.

Variation in number of founder boars affected the rate of increase of F in the first few years of selection but not thereafter (table 6), because effective population size after the foundation period was the same for all alternatives. Increase in F was very fast when number of founder boars was small. Increase of number of founder boars from one to five decreased F in year 25 by 7 percent. A further increase in number of founder boars changed F only moderately, because differences in effective population size between these alternatives were relatively smaller and because the restriction of population size was only temporary.

3.5 Effects of different selection intensities in selecting founder boars from a base population

Size of the base boar population determines possibilities for selection of founder boars. Effects of changes in size of the base boar population on optimal number of founder boars and on levels of response were investigated.

Use of just one founder boar generally offered some advantage in response in the first years of selection, but relative performance of this alternative diminished afterwards (figure 4). The initial disadvantage of alternatives with 15 founder boars relative to 5 founder boars decreased when number of base boars increased because differences in selection intensity between founder boar alternatives decreased. Differences in response between alternatives with 5 and 15 founder boars decreased with time because of a higher amount of additive genetic variance available for selection for alternatives with 15 founder boars. In the case of 60 or 90 base boars, it took 10 to 15 years to compensate for the initial disadvantage in response for alternatives with 15 founder boars.

Standard errors of mean responses over replicates for alternatives with 1, 5 and 15 founder boars, averaged over base boar alternatives, were 1.01, 0.74 and 0.66, which means that the value presented for the alternative with 15 founder boars and 30 base boars (table 6) was probably underestimated. Rates of increase of F were similar to values given for alternatives with the same number of founder boars in table 6.

Irrespective of size of the base boar population, use of five founder boars resulted in relatively good responses, not only in the first years of selection, but also after 25 years (figure 4). The risk of low response, though, was somewhat larger than for alternatives with 15 founder boars.

Effects of increasing selection intensity by means of selecting founder boars from a larger base boar population were also investigated. For each number of founder boars, changes in response relative to alternatives with 15 base boars are in table 7. Expected changes in response were calculated from eq. 8 with σ_I equal to Dfl. 4.14, the value that corresponded to selec-

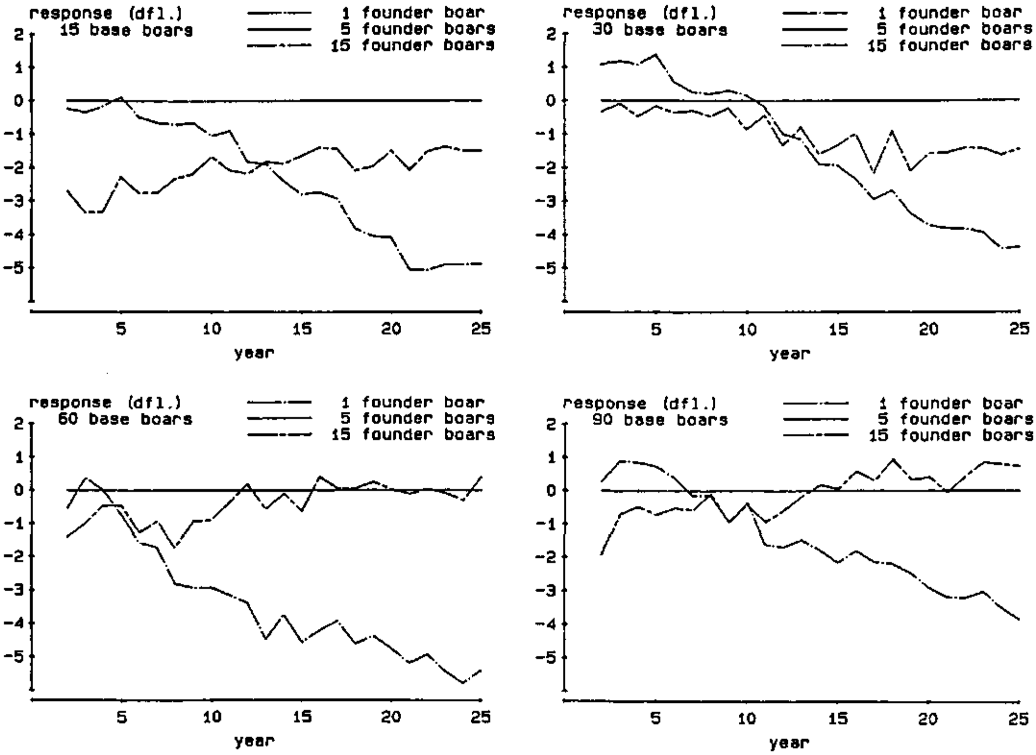

Figure 4. Cumulative response over time as a function of number of founder boars, for four numbers of base boars. Responses are deviations from cumulative response with 5 founder boars.

Table 7. Realized (R_r) and expected (R_e) cumulative response in year 25 as a function of number of base boars, for three numbers of founder boars. Values of R_r are deviations from cumulative response with 15 base boars.

No. of base boars	Number of founder boars 1		5		15	
	R_r	R_e	R_r	Re	R_r	R_e
30	0.30	0.64	-0.20	0.85	-0.18	1.61
60	-1.13	1.21	-0.59	1.57	1.28	2.59
90	0.95	1.52	-0.09	1.94	2.12	3.07

tion of boars (eq. 5). Just as with selection of founder sows (section 3.3), the relatively large variation in response between replicate lines complicated comparison of expected and realized responses. Table 7 shows that realized differences in response were generally smaller than expected. More intense selection among base boars reduced the between-sire variance component in offspring of founder boars and, thus, reduced prospects of further selection. The net benefit of more intense selection in base boars, thus, was smaller than expected from selection index theory.

3.6 Effects of changes in annual number of boars after the foundation period

To investigate the effects of an increase in effective population size after the foundation period, annual number of boars used for breeding was varied for alternatives with a founder population of 25 sows and 5 boars.

Differences between alternatives in the first years of selection (figure 5) originated from the small size of the founder population. Differences in cumulative response in year 25 between boar alternatives were not large (table 8). The changes of responses over time, however, were quite different (figure 5). For a herd of 100 sows, alternatives with five or ten boars annually had an initial advantage compared to 15 boars annually. This advantage was largest in years five to ten and diminished afterwards. A similar trend, but somewhat postponed, was observed for a sow herd of 50 sows (figure 5). Advantages of alternatives with five or ten boars annually, relative to 15 boars annually, increased up to year 21 and diminished after-

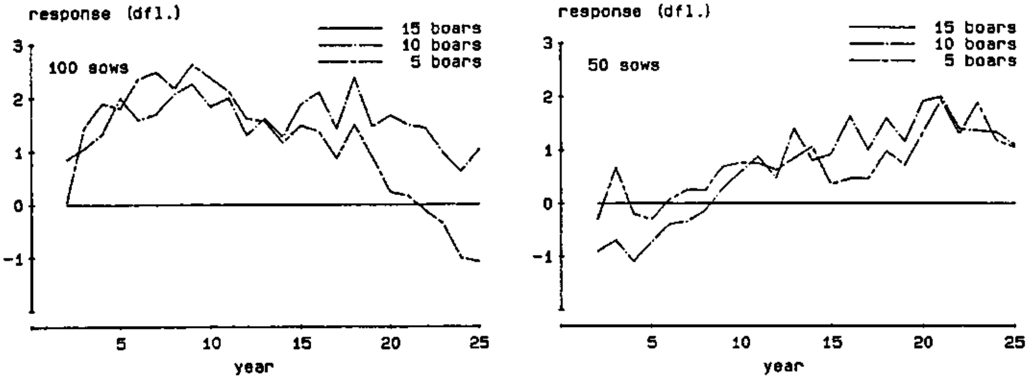

Figure 5. Cumulative response over time as a function of annual number of boars, for two sizes of the sow herd. Responses are deviations from cumulative response with 15 boars annually. Size of the founder population was 25 sows and 5 boars.

Table 8. Effects of changes in annual number of boars after the foundation period on cumulative response (R_{cum}), inbreeding coefficient and their standard errors (sem_R and sem_F) in year 25, on rate of increase in F (ΔF) and on additive genetic variance (V_A) lost because of selection and inbreeding.

Desired herd size	Number of boars	R_{cum}	sem_R	F	sem_F	ΔF in year		Reduction of V_A (%)[a]
						1-5	6-25	
50	5	58.90	.97	27.4	.34	1.19	1.35	33.9
50	10	58.95	1.21	19.7	.20	1.12	.87	28.3
50	15	57.85	.96	16.5	.16	1.09	.68	22.4
100	5	64.90	1.00	25.7	.25	1.09	1.26	34.6
100	10	67.01	1.02	18.2	.20	1.12	.78	26.4
100	15	65.98	.72	14.7	.16	1.09	.57	20.4

[a] Average reduction in V_A for growth rate, feed intake and lean percentage.

wards. This postponement was due to by larger differences in selection intensity between boar alternatives in case of 50 sows relative to a herd of 100 sows (De Roo, 1987b).

Boar alternatives also differed with respect to the level of inbreeding coefficient (table 8). Initial increases in F were similar because the founder population was of the same size for all alternatives. Increases in F after year five, however, were quite different. Selection and inbreeding decreased additive genetic variance available for selection most for alternatives with few boars annually (table 8). This explains the diminished advantage in response of these alternatives relative to 15 boars annually. Results are in agreement with De Roo (1987b).

3.7 General discussion

Determination of optimal size of the founder population implies not only taking account of mean breeding value and additive genetic variance in the founder group (James, 1971), but also the balancing of these factors. Optimal number of founder boars depends on differences in breeding values between boars available for selection. When these differences are small, it is advisable to start with a larger number of founder boars (10 to 20). Use of a small number of founder boars can be beneficial if their breeding value is extreme high. Such a strategy, however, bears risk. A boar's breeding value can be overestimated, which has an increasing impact on response with a decreasing number of founder boars. Secondly, even when the true breeding value of selected founder boars is high, use of just one to three founder boars may not be optimal, because it causes a fast increase of F in the first years of the breeding program. This means that the probability that favorable genes are lost by chance is large. Finally, genetic variance available for selection will be small when number of founder boars is restricted severely. Results showed that use of five founder boars provided, on average, good response. The established level of additive genetic variance offered good possibilities for further selection and a fast reduction of this variance was prevented.

Optimal number of founder sows is dependent on desired size of the sow herd. Results showed that a fast increase of number of sows towards the desired size of the herd is important because it is accompanied by a fast increase in number of litters tested and thus by an increase in selection possibilities. This aim can be reached by taking size of the founder sow population equal to 50 percent of the desired size of the sow herd. Inclusion of costs in the evaluation of alternatives, however, makes a gradual increase of size of the sow herd optimal. This means that a sow with a low performance should be culled, even if the desired size of the sow herd is not reached yet. To make this strategy optimal, completion of the build up of the sow herd should not be postponed longer than a couple of years. Optimal number of founder sows would, in such a strategy be lower than 50 percent of the desired size of the herd, because the increase of size of the herd is slowed down. A herd of 100 sows could, for example, be founded acceptably with 25 founder sows.

Even with a gradual increase of size of the sow herd, optimal number of founder sows will depend on desired size of the herd. Just as with selection of founder boars, the optimal number of sows also depends on differences in breeding value between sows available for selection and on accuracy of this breeding value.

A restriction of population size often occurs at the foundation of a new line but can also occur in an existing line because of, for example, a disease or a fire. Results showed that a temporary restriction of population size not necessarily diminished response as long as it was not too severe. An increase of effective population size after such a bottleneck affected response, as suspected by James (1971) and also the rate of increase in F.

The effect of selection on additive genetic variance (Bulmer, 1971, 1976) should not be ignored in comparison of breeding strategies, in agreement with Hill (1977) and De Roo (1987b). Every founder strategy will result in a different set of genetic parameters. The merit of each strategy depends not only on immediate gain from selection among base animals, but also on the level of these genetic parameters.

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Chapter 6

STUDIES ON BREEDING SCHEMES IN A CLOSED PIG POPULATION

4. Inbreeding depression

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ABSTRACT

A stochastic model was used to examine effects of inbreeding depression on selection response and inbreeding coefficient (F) in a closed swine herd. Three sets of partial regression coefficients of F on litter size at birth and at weaning and on growth rate were considered: no inbreeding depression, a set based on literature and a set of values twice as large as indicated by literature. Two sizes of the sow herd were considered, 25 and 100, and annual number of boars varied from 5 to 20.

Inbreeding depression induced a negative correlation between performance and F and, therefore, slightly diminished rate of increase in F when animals available for selection differed in F. Mild selection for litter size improved breeding values and, secondly, limited inbreeding depression for the trait. Selection counteracted inbreeding depression most effectively with a low rate of increase in F.

Inbreeding depression affected response for production traits most through its effect on the mean. Reduction in litter size had a limited effect on intensity of selection, because only two boars per litter were tested. This effect might be larger in other breeding programmes or less prolific species. Response was reduced when animals available for selection differed in F, because of a bias in estimated breeding values. Data to be used in estimation of breeding values, therefore, should be corrected for differences in F between animals.

Optimal annual number of boars was largely unaffected by degree of inbreeding depression. The main effect of inbreeding depression was to reduce response of alternatives with five boars annually relative to other boar alternatives. Even without inbreeding depression, number of boars used annually should be larger than five.

1. INTRODUCTION

An increase in the inbreeding coefficient (F) is inevitable in closed, finite populations. This increase in F affects response to selection in two ways. A fast increase in F corresponds to a large amount of drift, which causes random loss of genes and, thus, reduces additive genetic variance available for further selection. An increase in F, moreover, causes a decrease in heterozygosity and a reduction in the mean for traits subject to dominance, known as inbreeding depression (Falconer, 1981).

Inbreeding depression is important for components of fitness such as litter size and viability (Bowman and Falconer, 1960; Ablanalp, 1974; Falconer, 1981). Characters which are not closely connected with fitness, such as carcass characteristics or adult body weight, show little change when F increases (Falconer, 1981; Lamberson and Thomas, 1984; Pirchner, 1985). Inbreeding depression, however, might also affect response for production traits indirectly. Through its effect on reproduction, F might affect the number of animals available for selection and, thus, intensity of selection.

In pig nucleus breeding, selection and rate of increase in F are both important and affect each other. Selection invokes linkage disequilibrium and, thus, reduces the additive genetic variance available for further selection (Bulmer, 1971, 1976; Robertson, 1977; Fimland, 1979). Selection, moreover, increases the rate of increase in F (Robertson, 1961; Belonsky and Kennedy, 1987; De Roo, 1987b), which reduces the additive genetic variance and the mean for traits subject to dominance. On the other hand selection might be able to counteract inbreeding depression to some extent (Falconer, 1981). The interactions of selection and inbreeding need further investigation.

Effects of population size and selection intensity on selection response and F were studied by De Roo (1987b). This study, however, ignored inbreeding depression to avoid confounding of effects of F on the mean and on the additive genetic variance. The aim of this paper was to study effects of inbreeding depression on selection response and F over time. A model of a closed pig population (De Roo, 1987a) was used.

2. MATERIAL AND METHODS

2.1 Model

The model described by De Roo (1987a,b), evaluated changes in production and reproduction traits and inbreeding coefficient over 25 years of selection in a closed swine herd. Growth rate (23 to 100 kg), feed intake, lean percentage, litter size and interval from weaning to oestrus were incorporated in the model because of their economic relevance to pig breeders. The model included overlapping generations, continuous mating and farrowing and weekly selection of boars and sows. Week was the unit of time.

De Roo (1988) argued that an infinitesimal model, in which traits are affected by an infinite number of unlinked loci of small effect each, would provide useful information to pig breeding. An infinitesimal model that accounted for additive effects and inbreeding depression was used in this paper. Epistatic effects and dominance relationships between animals were ignored. Breeding values were generated as

$$A_i = 0.5 * A_j + 0.5 * A_k + \sqrt{(0.5 * CF)} * a * \sigma_A \qquad (1)$$

and $$CF = 1 - 0.5 * (F_j + F_k) \qquad (2)$$

where A_i, A_j, A_k: breeding values of individual i, its sire j and its dam k,
CF : correction factor that accounts for the expected reduction in additive genetic variance when parents have inbreeding coefficients F_j and F_k (Thompson, 1977),
a : random normal deviate,
σ_A : additive genetic standard deviation.

The relation between inbreeding depression and F is fairly simple when epistatic interactions between loci can be ignored, but becomes complicated when this assumption is not true (Crow and Kimura, 1970). Experimental results point to a linear relation between inbreeding depression and F (Falconer, 1981). With the assumptions of many unlinked loci affecting the trait and equal contributions of loci to the overall dominance effect, inbreeding depression effects for animals with the same F are similar. Phenotypes were simulated as

$$P_i = B + A_i + e * \sigma_E - bF * F_i \qquad (3)$$

where P_i : phenotypic value,
B : base level,
e : random normal deviate,
σ_E : environmental standard deviation,
bF : regression coefficient that reflects the degree of inbreeding depression.

2.2 Alternatives

Relatively little information was available on inbreeding depression. Required parameters were obtained from studies that were based on a considerable amount of data (Bereskin et al., 1968, 1970; Mikami et al., 1977; Leymaster and Swiger, 1981).

Inbreeding depression can be caused by a greater than zero inbreeding coefficient of the dam (F_D) or of the litter (F_L). Bereskin et al. (1968, 1970) concluded that F_D was responsible for the reduction of litter size at birth, the partial regression coefficient (bF) per 1 percent increase in F_D was .025 piglet, on average. F_D did not significantly affect litter size at weaning nor post-weaning traits when a correction for litter size at birth was made (Bereskin et al, 1968, 1970; Leymaster and Swiger, 1981). F_L did affect litter size at weaning, the value of bF was .023 piglet (Bereskin et al., 1968, 1970). Test growth rate was reduced significantly by F_L, bF was 2.0 $g.day^{-1}$ (Mikami et al., 1977; Leymaster and Swiger, 1981). Data of effects of F_L on feed intake capacity were lacking. Heterosis, which is complementary to inbreeding depression, is expected to have a favourable effect on feed conversion ratio (Sellier, 1976). A similar effect of F_L on feed intake and growth rate would leave feed conversion ratio unaffected. The value of bF for feed intake, therefore, was assumed to be zero. Leymaster and Swiger (1981) reported a slight negative effect of F_L on lean percentage, which means that a positive effect of F_L on side-fat thickness could be expected. Mikami et al. (1977), however, found a negative effect of F_L on this trait. Sellier (1976) concluded that heterosis effects on carcass quality traits were negligible. Values of bF for lean percentage and side-fat thickness, therefore, were assumed to be zero.

Three sets of values for bF (b0F, b1F and b2F) were studied in this paper. Set b0F refers to no inbreeding depression. Set b1F used estimates of bF, which were based on literature, values of bF for litter size at birth, litter size at weaning and for growth rate were .025 piglet, .023 piglet and 2.0 $g.day^{-1}$, respectively. The values of bF in set b2F were twice as large.

De Roo (1987b) used ovulation rate and prenatal survival as components of litter size. Bolet (1986) stated that ovulation rate did not show heterosis, contrary to prenatal survival. Inbreeding depression on litter size at birth, therefore, was simulated by means of a reduction of the survival probability of embryos up to birth, which depended on F_D. Inbreeding depression on litter size at weaning was simulated by means of a reduction of the survival probability of piglets up to weaning, which depended on F_L. Inbreeding depression for growth rate depended on F_L.

The rate of increase in F is largely determined by number of boars used per year (Wright, 1931; De Roo, 1987b). Annual number of boars, therefore varied, alternatives were 5, 10, 15 and 20 boars per year.

Possibilities for selection decrease when size of the sow herd decreases. Intensities of selection in a small herd, therefore, might be more sensitive to a change in litter size caused by inbreeding. Two sizes of the sow herd, 25 and 100 sows, were considered.

All combinations of level of bF, size of the sow herd and annual number of boars were evaluated. For each alternative, size of the founder population was 25 sows and 5 boars. Founder animals were selected from a base population of 75 sows and 30 boars. The mating policy in the foundation period was described by De Roo (1987d). Three boars were used simultaneously for breeding after the foundation period. Mating of relatives was avoided; maximum inbreeding coefficient of potential offspring was 0.125. If no potential mates met this requirement, least related individuals were mated. Twenty replicates were done for all alternatives.

2.3 Parameters and selection system

The model was applied to a sire line with characteristics as in table 1. It was assumed that 67 percent of sows that entered the breeding piggery farrowed. Probabilities that sows were culled at weaning for conformation or health problems were 10.0, 7.0, 7.5 and 10.0 percent for first, second, third, and fourth or greater parities. This culling was independent of the sow's performance for (re)production traits. Every week, a number of sows was selected for breeding. These sows came from the group of sows weaned in the previous week or from the pool of replacement gilts. Selection criterion was a performance index, that included production traits only.

Breeding goal (H) and selection index (I) were according to De Roo (1987a):

$$H = 0.178 * A_{GR} - 0.05 * A_{FI} + 3.0 * A_{LEAN} \tag{4}$$

$$I_{boars} = 0.0212 * P_{GR} - 0.0004 * P_{FI} + 1.5548 * P_{LEAN} \tag{5}$$

$$I_{gilts} = 0.0357 * P_{GR} - 2.5965 * P_{SF} \tag{6}$$

Table 1. General characteristics of nucleus breeding scheme.

General	
maximum number of parities per sow	5
length of suckling period (wks)	4.5
number of boars used simultaneously	3
size of pool of replacement boars	4
maximum stay in pool of replacement boars (wks)	11
maximum relationship of partners at mating	0.125
Performance test	
minimum litter size at weaning	6
minimum start growth (0 to 23 kg, $g.day^{-1}$)	300
maximum number of boars tested per litter	2
maximum number of gilts tested per litter	6
total number of testplaces in a division	50
minimum index at end of test, boars	85
minimum index at end of test, gilts	65
percentage of boars culled for conformation	40
percentage of gilts culled for conformation	20
Sexual maturity	
percentage of boars culled for reproduction or conformation	40
percentage of gilts culled for conformation	20

where A_i,P_i : breeding values and phenotypes for trait i,
GR : growth rate 23 to 100 kg ($g.day^{-1}$),
FI : feed intake ($g.day^{-1}$),
LEAN : lean percentage,
SF : side-fat thickness (mm).

Potential breeding animals were performance tested. Boars were fed ad libitum, whereas gilts were kept on a restricted diet. Only the animal's own performance data were included in the index. Variables in (5) and (6) were deviations from batch means. Index values were standardized at a mean level of 100 with a standard deviation of 32. In presentation of results, attention will be focussed on production traits in boars. Genetic and phenotypic parameters of production traits in the base population are in table 2.

Table 2. Genetic and phenotypic parameters of production traits in the base population.

Trait	Mean	h^2	σ_p	Correlations[a]		
				GR	FI	LEAN
growth rate (GR, $g.day^{-1}$)	900	.25	88	--	.85	-.15
feed intake (FI, $g.day^{-1}$)	2 400	.25	200	.65	--	-.35
lean percentage (LEAN)	52	.45	2.5	-.10	-.30	--

[a] Upper triangle: genetic correlations, lower triangle: phenotypic correlations

Lean percentage in boars was assumed to be estimated on live animals by means of modern equipment (R^2= 0.70). Breeding values for lean percentage were assumed to be normally distributed, phenotypes were expressed on a scale with a minimum of 35 and a maximum of 75 percent (De Roo, 1987a).

Selection of young breeding animals was a multi-stage process. At the end of the test a number of animals was culled for conformation and a relative mild selection on index was performed (table 1). At sexual maturity another number of animals was culled for conformation. In addition, a number of boars was culled because of a bad reproductive performance. For each sex, the animals with the highest indices among the remaining boars and sows were ultimately selected for breeding.

3. RESULTS AND DISCUSSION

3.1 Inbreeding coefficient (F)

Mean values of F of boars tested in year 25 are in table 3. With 25 sows, the level of inbreeding depression did not systematically affect F, nor its standard error. With 100 sows, the value of F slighly diminished with increasing bF and this effect was strongest with a small annual number of boars.

With 25 sows, the weekly number of sows that farrowed was small. Final selection of new breeding stock, therefore, tended to within family selection, which meant that F was not affected by selection. With 100 sows possibilities for selection were larger and inbreeding depression favoured

Table 3. Average inbreeding coefficient and its standard error in year 25 for three levels of inbreeding depression (b0F, b1F and b2F).

Number of sows	Number of boars	Mean			Standard error		
		b0F	b1F	b2F	b0F	b1F	b2F
25	5	28.8	28.9	28.9	.29	.27	.22
25	10	21.6	22.0	21.7	.20	.18	.20
25	15	19.1	19.0	19.5	.25	.22	.25
25	20	18.0	18.6	18.8	.13	.34	.22
100	5	25.7	25.6	25.1	.25	.22	.20
100	10	18.2	18.1	17.6	.20	.18	.11
100	15	14.7	14.8	14.5	.16	.13	.13
100	20	12.9	12.6	12.7	.11	.11	.11

selection of animals with a low F value. Number of families contributing to the group of potential replacement boars was largest with five boars annually because the time between subsequent moments of selection of boars was largest for that alternative. The effect of inbreeding depression on F, therefore, was largest with five boars annually.

With 100 sows, indirect selection on F diminished differences in F of tested boars between replicates, the standard error of the mean of F decreased with increasing bF when number of boars used annually was small. Differences in F between tested boars within replicate and year were already small because avoidance of mating of relatives was practiced (De Roo, 1987c) and these differences were not affected by bF.

3.2 Response for litter size

With no inbreeding depression, litter size at birth and at weaning were similar for all alternatives and averages over years 23 to 25 were 10.24 and 8.20, respectively. Averages over years 23 to 25 were used to reduce random year effects. Litter size at birth, thus, increased by 0.44 piglet in 24 years. This is due to mild selection on litter size at the start of the performance test (table 1) and to the higher probability for gilts from larger litters of being selected because number of tested gilts per litter increased with increasing litter size.

Cumulative responses for litter size at birth and at weaning for different levels of bF are in table 4. Selection kept litter size at birth up or above the level of the base population (9.80 piglets), except when effective population size was small. Because of a reduced survival probability of piglets up to weaning, however, litter size at weaning decreased relative to the base population level (7.84 piglets), except with moderate inbreeding depression and 20 boars annually.

Selection and inbreeding opposed each other. Observed response was adjusted for the expected inbreeding depression to compute a corrected effect of selection. For litter size at birth, these expectations were calculated from $bF*F_D$. Corrected cumulative response for this trait increased with an increasing effective size of the population (table 4). Calculation of th expected inbreeding depression was based on random mating, which means that all animals were assumed to have an equal probability of contributing to the next generation. Among sows with a similar F, selection

Table 4. Mean cumulative response (R_{cum}) and cumulative response corrected for inbreeding depression (R_{ccum}) for litter size at birth and at weaning of first parity sows, for two levels of inbreeding depression (b1F and b2F)[a].

Number of sows	Number of boars	Litter size at birth				Litter size at weaning			
		R_{cum}		R_{ccum}		R_{cum}		R_{ccum}	
		b1F	b2F	b1F	b2F	b1F	b2F	b1F	b2F
25	5	-.30	-.83	.36	.49	-.77	-1.81	.41	.45
25	10	.06	-.44	.56	.55	-.38	-1.26	.52	.51
25	15	.24	-.30	.67	.59	-.21	-1.04	.56	.56
25	20	.26	.00	.68	.84	-.20	-.82	.56	.70
100	5	-.12	-.71	.46	.42	-.58	-1.55	.56	.68
100	10	.15	-.24	.56	.56	-.29	-.89	.45	.55
100	15	.26	.22	.60	.88	-.12	-.53	.48	.65
100	20	.36	.06	.65	.65	.01	-.53	.53	.52

[a] Results were averaged over years 23 to 25, mean levels in the base population were 9.80 and 7.84 piglets per litter.

favoured those with highest breeding values for litter size and, thus, avoided part of the expected loss in performance. When rate of increase in F increased, selection had less possibilities to discriminate between animals with the same F, in agreement with Eisen and Hanrahan (1974) and Falconer (1981).

Expected changes in litter size at weaning were calculated as 80 percent of the expected change in litter size at birth plus the direct inbreeding depression effect on survival probability of piglets up to weaning. This 80 percent is the average survival probability of piglets up to weaning for first parity sows in the base population. Selection had a positive effect on litter size at weaning, as expected from its effects on litter size at birth (table 4). Effects of selection on litter size at weaning were expected to be 80 percent of the effects of selection on litter size at birth because survival probability of piglets up to weaning was simulated as a trait with no additive genetic variance (De Roo, 1987a). With a small number of boars, however, these effects were larger than expected. Because of a decrease in litter size at birth, which was largest with a small number of boars, survival probabilities of piglets up to weaning increased (De Roo, 1987a). Reduction of litter size at weaning, therefore, was limited.

3.3 Response for production traits

Cumulative response for growth rate in year 25 is in table 5. Response diminished considerably when bF increased. This effect was largest with a small number of boars, as expected. With 100 sows, cumulative response corrected for inbreeding depression (R_{ccum}) diminished with increasing bF and this effect was largest with a small number of boars (table 5). With 25 sows, R_{ccum} was not affected by bF, except with five boars annually. The decrease in R_{ccum} with increasing bF and a small number of boars could be due to the decrease in litter size and, thus, in selection possibilities for these alternatives. The fact that bF affected R_{ccum} with 100 sows and not with 25 sows when annual number of boars was larger than five, however, can not be explained by changes in litter size. Because intensities of selection were smallest with 25 sows, these were also most sensitive to changes in number of animals available for selection. This means that a change in litter size would have largest effects on response in a herd of 25 sows.

Inbreeding depression not only affected mean growth rate, but also complicated selection. Breeding values of animals were not corrected for

Table 5. Mean cumulative response (R_{cum}) and cumulative response corrected for inbreeding depression (Rccum) for test growth rate in year 25, for three levels of inbreeding depression (b0F, b1F and b2F)[a].

Number of sows	Number of boars	R_{cum}			R_{ccum}		
		b0F	b1F	b2F	b0F	b1F	b2F
25	5	103	42	-24	103	100	96
25	10	111	77	22	111	121	109
25	15	107	71	20	107	109	98
25	20	85	69	12	85	106	87
100	5	161	85	44	161	136	144
100	10	168	127	69	168	163	139
100	15	163	122	91	163	152	149
100	20	162	123	103	162	148	154

[a] Mean level in the base population was 900 $g.day^{-1}$.

differences in F between animals, which means that estimated breeding values were biased. This bias was largest, when differences in F between animals were largest. With 25 sows the weekly number of sows that farrowed was small and final selection of new breeding stock tended to within family selection. The bias in estimated breeding values due to inbreeding depres sion, therefore, affected selection less. With 100 sows, animals available for selection came from a larger number of families and the greater bias in estimated breeding values reduced the efficiency of selection.

Response for feed intake and lean percentage was expected to be unaffected by bF, except when a change in litter size would cause a change in selection intensities or when the bias in estimated breeding values for growth rate would cause selection of different animals. With 25 sows, response for feed intake was not clearly affected by bF (table 6). With 100 sows, cumulative response decreased with increasing bF. The bias in estimated breeding values for growth rate reduced response for that trait and had a correlated negative effect on feed intake. Response for lean percentage was not affected by bF for neither size of the sow herd (table 6), because of the low correlation with growth rate.

Table 6. Mean cumulative response (R_{cum}) for feed intake and lean percentage in year 25 for three levels of inbreeding depression (b0F, b1F and b2F)[a].

Number of sowa	Number of boars	Feed intake			Lean percentage		
		b0F	b1F	b2F	b0F	b1F	b2F
25	5	-20	-10	-37	9.29	8.90	9.43
25	10	-1	4	-11	8.99	9.04	8.73
25	15	-20	0	-12	7.89	7.39	7.65
25	20	-34	-7	-32	6.87	7.16	6.91
100	5	28	-30	9	12.55	12.53	12.19
100	10	16	11	-30	12.63	12.77	12.43
100	15	3	-9	-15	12.33	12.44	12.42
100	20	29	-19	5	11.91	12.06	11.86

[a] Mean levels in the base population were 2 400 $g.day^{-1}$ and 52.0 percent.

3.4 Overall response

Overall response was expressed in Dfl. using economic weights from eq. 4. Response curves as a function of bF, for different numbers of boars and sows, are in figure 1. With no inbreeding depression, response was curvilinear with time because of a loss of additive genetic variance due to increased genetic relationships between animals (De Roo, 1987b). Annual genetic improvement, thus, diminished with time. Inbreeding depression, on the other hand, increased fairly linear with time due to the almost linear increase in F. Curvilinearity of response, therefore, increased with increasing bF, in agreement with theory (e.g. Bohren, 1975). Response curves became rather flat with a small effective population size and a high bF.

Mean cumulative responses in year 25, their standard errors and expected and realized reductions in response due to inbreeding are in tables 7 and 8. Reductions in response were substantial. Despite somewhat lower values of F in the case of 100 sows, absolute reductions in response with a given annual number of boars were similar for both herd sizes. The bias in estimated breeding values for growth rate increased the effect of inbreeding on response with 100 sows (table 5). Relative reductions in response, how-

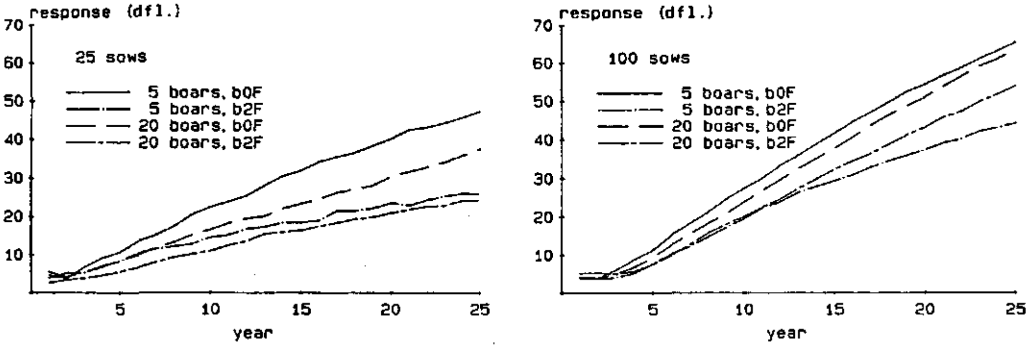

Figure 1. Cumulative response over time as a function of level of inbreeding depression and annual number of boars for herds of 25 and 100 sows.

Table 7. Mean cumulative response (R_{cum}, in Dfl.) in year 25 for three levels of inbreeding depression (b0F, b1F and b2F) and reductions in R_{cum} (R_F) relative to no inbreeding depression (in percent).

Number of sows	Number of boars	R_{cum}			R_F	
		b0F	b1F	b2F	b1F	b2F
25	5	47.28	34.65	25.92	26.7	45.2
25	10	46.76	40.57	30.69	13.2	34.4
25	15	43.75	34.80	27.08	20.5	38.1
25	20	37.50	34.07	24.41	9.1	34.9
100	5	64.90	54.14	43.93	16.6	32.3
100	10	67.01	60.38	51.13	9.9	23.7
100	15	65.98	59.50	54.29	9.8	17.7
100	20	63.09	59.05	53.64	6.4	15.0

ever, were largest with 25 sows because possibilities for selection were lower with that herd size (table 7).

Optimal annual number of boars depended on population size (table 7, figure 2). The main effect of inbreeding depression was to reduce response of alternatives with five boars annually relative to other boar alternatives. With 25 sows and no inbreeding depression, initial response was

Table 8. Standard errors of mean cumulative responses in year 25.

Number of boars	25 sows			100 sows		
	b0F	b1F	b2F	b0F	b1F	b2F
5	1.21	1.08	1.51	1.00	.63	.83
10	.89	1.05	1.15	1.02	.79	.81
15	1.28	1.21	1.19	.72	.83	.73
20	1.36	.76	.80	.74	.69	.91

highest with five boars annually. The advantage relative to ten boars annually, however, diminished with time (figure 2). Inbreeding depression made ten boars annually optimal with 25 sows. The intensity of selection was so much larger than with 15 or 20 boars annually, that response was highest with ten boars annually, despite a somewhat larger inbreeding depression.

Differences in intensity of selection between boar alternatives were smaller and differences in F were larger with 100 sows, increasing response with a larger annual number of boars relative to five boars annually. Even without inbreeding depression, use of five boars annually had no advantage anymore over ten boars annually, not even in the early years of selection. Advantages of intense selection in short-term response were less than expected from theory because of reduced genetic variance from linkage disequilibrium and reduced selection intensity from small numbers of families (De Roo, 1987b). Response with five boars annually decreased with increasing bF. Differences between other boar alternatives decreased (figure 2) and became very small relative to standard errors of means over replicates (table 8).

3.5 General discussion

Inbreeding depression and heterosis are complementary (Falconer, 1981). If the initial frequency of heterozygotes is high, the possible loss due to inbreeding is also high. Similarly, if the constituting lines of a cross have drifted far apart, the F1 cross will exhibit a large amount of heterosis for traits subject to dominance because of high frequencies of heterozygotes. Inbreeding depression effects, thus, depend on initial frequencies of heterozygotes and differ between populations. Correction for inbreeding

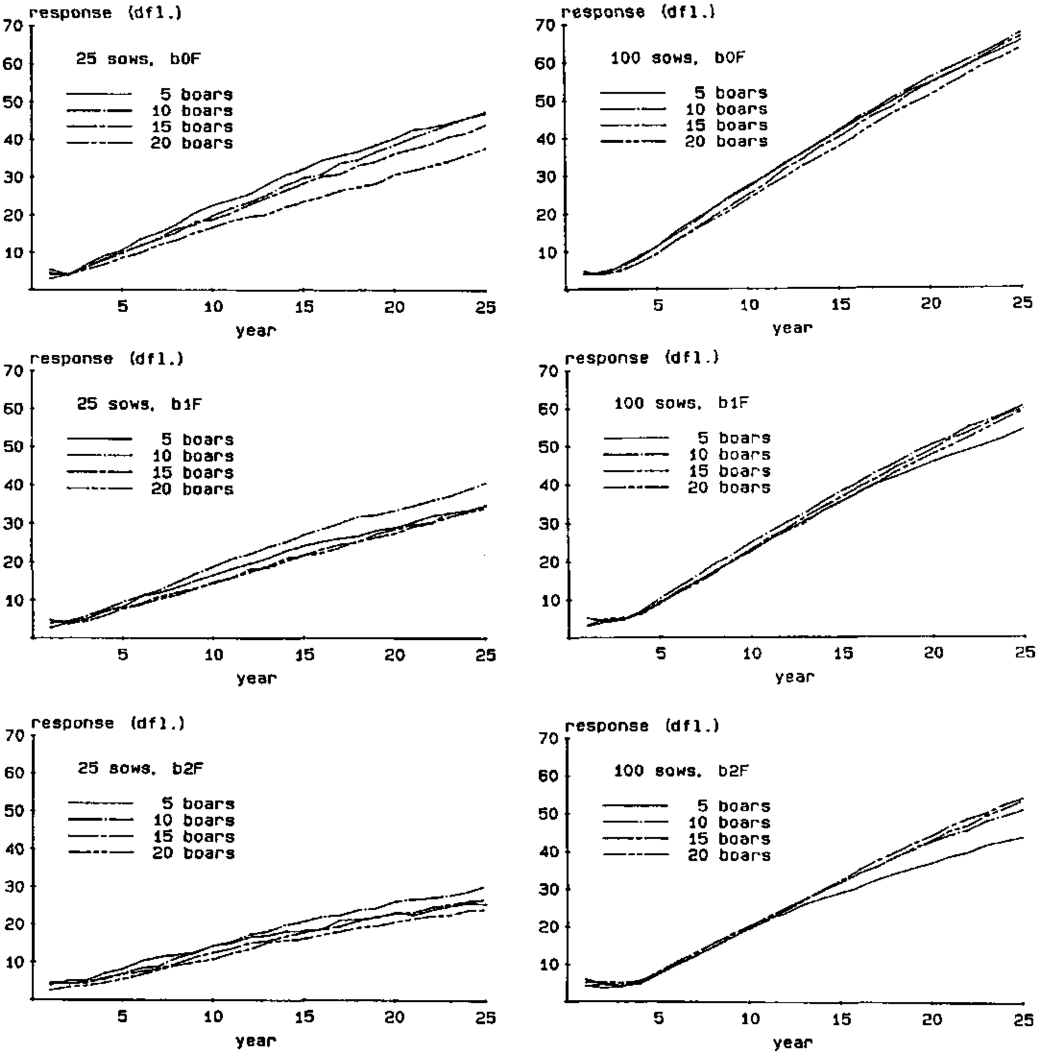

Figure 2. Cumulative response over time as a function of annual number of boars for three levels of inbreeding depression and herds of 25 and 100 sows.

depression requires knowledge of the values of bF of the population under selection.

Dominance effects were assumed to be caused by many loci of small effect each. This is a simple model and it might be more realistic to assume a distribution of dominance effects with few loci with large effects and many loci with small effects, as suggested by Hill (1985) for additive effects. There is little information, however, on which to base such a distribution. Selection can be expected to maintain loci with large dominance effects as heterozygotes, at least when their number is small (Falconer, 1981). Observed inbreeding depression would then be caused by the remaining loci with a small dominance effect each. Experiments of Bowman and Falconer (1960) and Ablanalp (1974) have provided evidence that a simple dominance model is adequate for litter size. Several lines became extinct in these experiments, but the reproductive performance of the remaining lines did not diminish. This would not have been possible in the case of overdominance because selection would then not have been able to create a homozygous line that was as good as the non-inbred population. A model with many loci of small effect each, therefore, can provide useful information on inbreeding depression effects.

Inbreeding depression effects were assumed to be equal for animals with the same F. This assumption requires an infinite number of loci. More general, inbreeding depression is a function of F and the number of loci (n). The expected number of homozygote loci is F and its variance is F(1-F)/n. Differences in inbreeding depression effects between litter mates offer the possibility of selecting the most heterozygous animals. Such differences, however, complicate selection. Performance can be due to breeding value or to degree of heterozygosity. In the latter case, performance of offspring of high producing parents, on average, will be less than expected. This bias in estimated breeding value can not be corrected and will diminish response.

Inbreeding depression can affect response directly, through its effect on the mean, but also through its effect on fitness, and, thus, on intensity of selection as shown by Ercanbrack and Knight (1981, 1983) for sheep. The reduction of litter size due to inbreeding depression had little effect on response in the present study. A limited effect of reduced litter size was expected, because number of boars tested per litter was limited to two. Even with a reduced litter size, it was in most cases still possible to test two boars per litter. The impact of reduced litter size on response would be larger when all boars in a litter were tested. A similar conclusion applies to less prolific species as horses, cattle or sheep.

Inbreeding is also expected to affect secondary fertility traits as reproductive performance of boars, percentage of sows that show heat, percentage of sows pregnant after first mating, etc. These inbreeding effects will reduce response because number of animals available for selection will be reduced. The effects of inbreeding on secondary fertility traits were ignored because the range of values of bF was assumed to give a good indication of possible inbreeding depression effects.

Inbreeding depression caused a bias in estimated breeding values when animals available for selection differed in F. A mating system that avoids the mating of relatives limits differences in F between animals (De Roo, 1987c) and, therefore, is expected to limit bias in estimated breeding values. Such a mating strategy was practiced and it did not prevent bias. Without avoidance of mating of relatives, however, the bias would have been larger. The bias diminished response (table 5). It is, therefore, advisable to correct data to be used in the estimation of breeding values for differences in F.

Optimal annual number of boars was largely unaffected by degree of inbreeding depression (figure 2). Even without inbreeding depression, number of boars used annually should be larger than five (De Roo, 1987b). This conclusion was strenghtened by the inclusion of inbreeding depression effects.

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Chapter 7

GENERAL DISCUSSION

Optimization of breeding schemes involves consideration of many factors (Harris et al., 1984). An optimal breeding scheme leads to continuous genetic improvement over the period of time of interest to animal breeders. Efficient use of available additive genetic variance in a finite population is difficult because selection and increasing additive genetic relationships between animals affect both the mean and the additive genetic variance.

The modelling approach followed in this thesis facilitated study of different breeding schemes. The genetic model used was highlighted in the first chapter. This model applied to quantitative traits and assumed that many loci of small effect each affected a trait. As an example of a finite population in which selection and inbreeding both are relevant, a pig nucleus herd was modelled (chapter 2). This model was used to study effects of population size and selection intensities (chapter 3), mating policy (chapter 4), size of the founder population (chapter 5) and inbreeding depression (chapter 6) on selection response and inbreeding coefficient (F). Parameters used applied to a sire line.

Implications of the study for the design of breeding schemes in general and, more specific, for selection in some livestock species are discussed in this chapter. Effects of opening of the nucleus and breeding programmes that aim at conservation of animal genetic resources are also considered.

1. IMPLICATIONS FOR THE DESIGN OF BREEDING PROGRAMMES

The selection policy that will yield optimum results depends on the true genetic model. Very intense selection would be justified with free recombination, a low number of loci and high frequencies of desirable genes (Robertson, 1970). A similar conclusion holds when differences in gene effects between loci are large. In this thesis breeding values of traits were simulated using normal deviates. This assumes a large number of loci and intermediate gene frequencies. Selection then hardly changes the average gene frequency and the equilibrium additive genetic variance (Falconer, 1981). With low initial gene frequencies, selection causes a relative large increase in additive genetic variance and response to selection will be higher than expected from a model with normal deviates. With high initial gene frequencies, selection will decrease additive genetic variance and response will be lower than expected from a model with normal deviates. In summary, results of this study apply to traits affected by a considerable number of loci, with intermediate gene frequencies, small differences in gene effects between loci and no epistasis.

Selection and inbreeding both affect the additive genetic variance. Selection induces linkage disequilibrium (Bulmer, 1971). Every new round of selection will add to the amount of linkage disequilibrium that already existed. Some of the variance lost previously, however, will be regenerated by recombination. After a number of generations of selection, the reduction in variance due to linkage disequilibrium will reach an equilibrium value (d^*). Bulmer (1971) and Fimland (1979) developed a formula to compute d^*:

$$d^* = \sigma_0^2 * [2*k*h_0^2 - 1 + \sqrt{(1 - 4*k*h_0^2*(1 - h_0^2))}] \ / \ (2*(1 - k)) \qquad (1)$$

where σ_0^2 : phenotypic variance in the base population,
k : relative change in phenotypic variance caused by one round of selection,
h_0^2 : heritability in the base population.

This formula requires the assumption of an infinite population size. If the phenotype is normally distributed in the parent generation, k is $-i(i-x)$, where i is the intensity of selection and x is the standard normal deviate that corresponds to p, the proportion selected (Bulmer, 1971). Magnitude of the effect of selection on the additive genetic variance depends on intensity and accuracy of selection. As an illustration, effects of variation in selection intensity and heritability on d^* and on the genetic improvement are in table 1. Responses to selection were computed according to $i * h^2 * \sigma_p$. The environmental variance was assumed constant over time.

Genetic improvement accounting for reduction in variance due to linkage disequilibrium (R^*) was considerably less than genetic improvement assuming constant variance (R). Linkage disequilibrium, therefore, should not be ignored in the computation of benefits of breeding schemes. The heritability had a large impact on amount of linkage disequilibrium and, thus, on response. More general, accuracy of selection is important with respect to reduction in variance due to linkage disequilibrium (Fimland, 1979). Proportion of animals selected varied from 38 percent (i= 1.0), 20 percent (i= 1.4) to 6 percent (i= 2.0). Within this range, variation in intensity of

Table 1. Stabilized values of linkage disequilibrium (d^*), phenotypic variance (σ^2) heritabilities (h^2) and genetic improvement (R^*) as a function of intensity of selection (i) and initial heritability (h_0^2). R^* is compared to R, response to selection assuming constant variance[a].

	h_0^2=.25			h_0^2=.50			h_0^2=.75		
	i=1.0	i=1.4	i=2.0	i=1.0	i=1.4	i=2.0	i=1.0	i=1.4	i=2.0
d^*	-.034	-.037	-.040	-.117	-.125	-.133	-.240	-.256	-.271
σ^2	.966	.963	.960	.883	.875	.867	.760	.744	.729
h^2	.224	.221	.219	.434	.429	.423	.671	.664	.657
R^*	.220	.302	.429	.408	.562	.788	.585	.802	1.122
R	.250	.350	.500	.500	.700	1.000	.750	1.050	1.500
R^*/R	.880	.863	.857	.815	.803	.788	.780	.764	.748

[a] The initial phenotypic variance is 1.000

selection had limited effects on d^* and on the ratio R^*/R. Equation 1, however, refers to an infinite population size. De Roo (1987a) considered a finite population and showed that responses of alternatives with intense selection (5 sires annually or 7 sires per generation) were considerably overestimated by short-term selection theory (Cunningham, 1969). Average annual genetic improvement over 25 years was about 70 percent of the initial genetic improvement (De Roo, 1987a, table 8), whereas heritabilities were around .3. According to table 1, linkage disequilibrium limits response to about 85 percent of the initial genetic improvement in that case. The observed extra reduction in response is due to increased additive genetic relationships between animals. This makes mating of relatives inevitable and reduces the additive genetic variance. On the other hand, intensities of selection are reduced. This effect is strongest with few families and intense selection (Hill, 1976, 1977). Effects of increases in additive genetic relationship between animals on additive genetic variance and on intensity of selection are significant and should be considered in comparisons of breeding programs.

Equation 1 could be used to correct obtained genetic parameters for the effect of selection. The formula, however, assumes that intensity of selection is constant over time which is not correct in finite populations. A decrease in selection intensity will cause a reduction in amount of linkage disequilibrium. In a finite population, therefore, linkage disequilibrium builds up in the early years of selection, reaches a maximum and diminishes steadily afterwards. Additive genetic variance available for selection, however, will not increase over time because of increases in F. Development of a method that accounts for effects of selection and increases in F on additive genetic variance and on selection intensity, deserves further investigations. Mueller and James (1983) used a step-wise procedure and computed variances per generation. Such a method should be preferred over use of eq. 1. The average inbreeding coefficient of parents probably could be used to account for the effect of inbreeding on the additive genetic variance.

In this study, selection was based on individual performance data of the animal. Including family information in the index or BLUP procedures would improve accuracy of selection and, thus, initial response. The amount of linkage disequilibrium, however, would also increase (table 1), reducing the advantage of higher accuracy. Short-term selection theory (Cunningham, 1969), thus, overestimates benefits of including family information in a selection index. In the case of a finite population, the overestimation would be larger, because an increase in accuracy of selection causes an increased rate of increase in F.

Selection affects the between-family variance, but not the within-family variance due to segregation. Response to within-family selection relative to mass selection, therefore, is underestimated by short-term selection theory. In the case of a finite population, within-family selection is even more profitable, because it reduces the rate of increase in F (Hill, 1972). Response to within-family selection will especially be large with large family sizes (Dempfle, 1975) and needs further investigation.

Optimal size of nucleus lines depends on differences between benefits, obtained from the sale of breeding animals, and costs of managing a nucleus herd. Increases in size of a nucleus line will increase response to selection because of increases in number of animals available for selection. Response does not increase linearly with size of the nucleus line. Increase in response diminishes with increasing herd size (De Roo, 1987a). An increase in herd size might be worthwhile if an increase in breeding value has a positive effect on the sales price of breeding animals or on the market share of the breeding company. Benefits that can be obtained depend on the magnitude of these effects.

Response to selection depends on intensity and accuracy of selection. When selection is for traits with high heritabilities, use of information from relatives adds relatively little to the accuracy of selection. Including family information will have a greater impact when initial accuracy is low, as for example for fertility traits. When number of sires does not increase proportionally to number of dams, number of relatives and, thus, accuracy of selection, increases with increasing population size. Response to selection, therefore, can increase with increasing population size because of an increased intensity of selection but also because of an increased accuracy of selection. The latter is especially relevant in the case of a dam line. Optimal population size for a dam line, therefore, will be larger than for a sire line.

De Roo (1987a,d) showed that in an optimal breeding scheme for a swine nucleus herd 10 to 20 boars should be used annually, depending on size of the sow herd. This means that 13 to 26 boars should be used per generation. These numbers are relevant to other species, but some remarks are necessary. There is no single optimal number of sires that will always provide best results. Instead, a range of numbers of sires is expected to result in similar responses. This range depends on number of animals available for selection, which is a function of number of dams to breed sires and of prolificacy of the breed. With few animals available for selection, optimal number of sires per generation is approximately 15. If number of animals available for selection increases, the range of optimal numbers of sires widens and includes larger numbers of sires.

Optimal number of sires also depends on accuracy of selection. BLUP improves accuracy of selection but can lead to a high rate of increase in F (Belonsky and Kennedy, 1987). BLUP takes account of breeding values realized in the past, but it does not consider future possibilities of forming new, favorable combinations of genes. BLUP, therefore, should be applied with the restriction that sufficient genetic variance should be maintained to enable further genetic improvement.

Optimal number of sires finally depends on aim of the breeders. If conservation of genetic variance is of some concern, optimal number of sires will increase. Breeding schemes that aim at conservation of animal genetic resources are discussed in section 3.

The mating system will affect the additive genetic variance (Falconer, 1981; De Roo, 1987b). Inbreeding leads to an increase in between-family variance relative to random mating, whereas the within-family variance decreases. Net result is an increase in genetic variance available for selection. This conclusion, however, only holds within a generation. The best families will contribute most to the next generation of offspring. Additive genetic variance, therefore, will decrease over generations when inbreeding and mass selection are combined. Moreover, increases in F will initially be fast, which might lead to fitness problems. The risks of inbreeding make this mating system unattractive. Maximum avoidance of inbreeding, on the other hand, reduces the additive genetic variance within a generation and has little effect on the rate of increase in F when effective size of the population is large enough (De Roo, 1987b). A mating system in which mating of full and half sibs is avoided probably is preferable.

Determination of optimal size of a founder population implies a balancing of mean breeding value and additive genetic variance in the founder group (De Roo, 1987c). Optimal number of founder animals depends on differences in estimated breeding values between animals, on accuracy of these estimates and on the risk of low response a breeder is willing to take. This risk increases with a decreasing number of founder animals.

Effects of a temporary restriction of population size on selection response depend on number of and genetic relationships among remaining animals. A fast increase in effective population size after such a bottleneck can limit the rate of increase in F and the negative effects on response.

In a sire line, emphasis is on improvement of additive genetic values. The level of F is relevant to breeders because it affects the additive genetic variance. Direct effects of inbreeding depression on production traits are less important in a sire line because a loss in heterozygosity will be regained in hybrid slaughter animals. Inbreeding depression, however, might also affect selection response indirectly. Through its effect on fertility, inbreeding depression will affect number of animals available for selection and, thus, selection response. This effect will be largest when a relative large number of offspring is required for replacement and, therefore, is expected to be larger in sheep or cattle than in swine.

With differential inbreeding, effects of inbreeding depression will differ between animals and estimated breeding values will be biased (De Roo, 1987d). A mating system that avoids mating of relatives can limit this bias because it reduces differences in F between animals (De Roo, 1987b). It is preferable, however, to correct data to be used in estimation of breeding values for differences in F between animals. This requires estimation of effects of inbreeding depression.

2. OPENING OF THE NUCLEUS

It is questionable whether a nucleus population will be kept closed for 25 years. Animals can be imported from lower tiers in the production pyramid, known as open nucleus breeding systems (James, 1977). Animals can also be purchased in other countries or from other breeding companies. James (1977) considered open nucleus breeding systems. He concluded that the rate of genetic gain obtained from opening the nucleus was only appreciable when about 50 percent or more of females born had to be selected as replacements. This gain was expected to be 10 to 15 percent of the gain in a closed nucleus. James (1977) stated that the rate of inbreeding in an open nucleus would be about half of that in a closed nucleus of the same size. James considered a discrete generation model and ignored effects of selection and inbreeding on the additive genetic variance. He assumed accuracy of selection equal in base and nucleus. Mueller and James (1983) considered effects of loss of genetic variance due to linkage disequilibrium and increase in genetic variance due to mixing base and nucleus born animals. Constant variance theory (Cunningham, 1969) overestimated response considerably but approximated advantages of opening the nucleus rather well. Increases in genetic variance due to mixing groups with different breeding values turned out to be insignificant with respect to optimum transfer rates between nucleus and base population. Hopkins (1978) extended the method of James (1977) to overlapping generations and different accuracies of selection in base and nucleus. He concluded that almost no base-born females should be selected as nucleus replacements when selection in the nucleus was more accurate.

Import of animals from other populations can be considered if their breeding values are expected to be above those of nucleus-bred animals. Exhaustion of genetic variance or inbreeding depression can be other reasons for import of foreign animals. Superior animals from lower tiers in the production pyramid probably can be used directly in the nucleus, because their genetic background is known. Animals from other populations, however, probably first will be tested in an experimental line. Such a line uses test capacity, which otherwise could be used for the nucleus and, therefore, has a negative effect on genetic improvement in the nucleus. Possibilities for selection in an experimental line will be limited because of its restricted size (De Roo, 1987a). It is not profitable, therefore, to keep such a line as an independent breeding unit for many years. Animals from an experimental line that show a high performance relative to the nucleus should be used in the nucleus on short term. The remaining animals should be culled, thus making all test capacity available again to the nucleus.

In conclusion, introduction of new breeding animals from outside the nucleus is only worthwhile occasionally. The effect on selection response and F will be limited and the selection policy followed in the nucleus will be of major importance to benefits of the breeding scheme.

3. CONSERVATION OF ANIMAL GENETIC RESOURCES

The breeding scheme to be applied in a finite population depends on aim of the breeders (De Rochambeau and Chevalet, 1982). When selection and inbreeding both are relevant, as in this thesis, the breeding scheme will differ from a situation with emphasis on genetic conservation. In the latter case, the main objective is maintenance of genetic variance, not maximization of selection response. Interest in conservation of animal genetic resources is increasing (FAO/UNEP, 1981; Maijala et al., 1984). Economic objectives of selection might change in the future because of a change in husbandry or marketing needs (Smith, 1985). Breeding stock, selected for current breeding objectives might not be able to meet these changed requirements. Concern about loss of genetic variance is increasing because of a trend of worldwide concentration on few specialized stocks (Smith, 1984a). This trend is most clear for poultry where a few large breeding companies dominate the world market (Crawford, 1984), but a similar trend might be expected for swine. In dairy cattle, the influence of the Holstein breed is increasing (Cunningham, 1983) and further development of reproductive technologies (Nicholas and Smith, 1983) might lead to further specialization.

The uncertainty of future breeding objectives justifies the development of a large number of alternative lines, each selected for a specific objective (Smith, 1985). Development costs would be small relative to expected benefits and genetic conservation by means of storage of frozen semen would be cheapest (Smith, 1984b). Genetic conservation, however, is unattractive to breeding companies or individual breeders because of uncertainty of future benefits. Conservation activities, therefore, need to be designed on a national or, probably, international scale. A first step in the process of genetic conservation is evaluation of available genetic resources. Next is identification of important traits of different breeds and strains as performed by Maijala et al. (1984) and the decision which populations need to be maintained. Finally, a conservation strategy needs to be chosen. Many finite populations need to be maintained as live breeding stock because of, for example, cultural or aesthetic reasons (Crawford, 1984; Smith, 1984a) or because conservation by means of frozen semen or embryos is not possible yet. Breeding schemes that aim at maintenance of genetic variance will be discussed.

Theoretically, loss of genetic variance would be minimized if the population would be split in a large number of independent lines (Robertson, 1964). Genes lost by chance in one line are likely to be present in another line. A large part of the original genetic variance could later be restored by crossing. Benefits of such a system, however, would not become apparent until after many generations. The increase in relationship between animals within a line initially would be fast and the risk of loss of lines because of fitness problems would be large (Falconer, 1981). A more reasonable approach, therefore, is to subdivide the population in a limited number of sublines and apply circular mating (Kimura and Crow, 1963). In such a scheme males selected in one subline are mated to females from another subline. Two kinds of schemes are distinguished (De Rochambeau and Chevalet, 1982), fixed schemes in which males of subline i always mate to females of subline j and cyclical schemes in which these combinations of sublines with respect to mating are a function of time. Cyclical schemes turn out to be more effective in the short term when number of sublines is larger than ten, fixed schemes might be better with fewer sublines and are theoretically expected to be better in the long term (De Rochambeau and Chevalet, 1982). Circular mating can be a practical solution to the problem of conservation of genetic variance when the population is spread over a large number of geographically distinct herds. A cyclical scheme than has the advantage that it buffers genetic differences between herds (De Rochambeau and Chevalet, 1982).

Circular mating is in fact a way to equalize family size on the male side and to avoid mating of relatives. Similar results, therefore, can be expected from a method in which the population is not subdivided and in which strict within-family selection is practiced in combination with maximum avoidance of mating of relatives. Strict within-family selection implies that every sire contributes exactly one son and a fixed number of daughters to the next generation of breeding animals and every dam contributes one daughter and no more than one son to the next generation.

Irrespective of whether the population is subdivided, number of males and females used per year and length of generation interval are important with respect to rate of increase in F (Hill, 1972). Smith (1984a) argued that, with frozen semen, sires could rotationally be used on each others daughters and stated that this would lead to a low rate of inbreeding. Chevalet and De Rochambeau (1985), however, showed that this method resulted in a large loss of genes originally present in female founders. The contribution of individual sires was undesirably high in the method proposed by Smith (1984a). The generation interval, therefore, should not be prolonged by means of a prolonged use of sires.

When number of males is, much smaller than number of females, rate of increase in F can be reduced by using males for a short time only, thus increasing number of males used per generation. The increase in number of males causes an increase in effective population size despite shortening of the generation interval (chapter 3, eq. 14). An increase in effective population size could also be obtained from an increase in number of males simultaneously used for breeding. Such an alternative, however, probably would be more costly.

The generation interval could be lengthened by postponing use of males until old age. Such a policy, however, requires the retaining of a large number of males, which means that at similar costs a larger number of young males could be used. The latter is more effective with respect to increase in effective population size and, thus, with respect to conservation of animal genetic resources. Females should be used for breeding until old age, thus enlarging the generation interval. Different policies for different sexes are paradoxical, but the method equalizes contributions of males and females to the next generation.

4. SPECIFIC IMPLICATIONS FOR OTHER LIVESTOCK SPECIES

4.1 Poultry

Commercial poultry breeding is dominated by a few large breeding companies (Crawford, 1984). Distinction should be made between selection in egg producing poultry and in broiler producing poultry. Egg laying poultry have been under selection for many generations. Further improvement of egg production in layers is difficult, because of low heritabilities, antagonisms between traits, such as egg number and egg quality, and forces that oppose selection, such as inbreeding and natural selection (King, 1981). Flock (1980), however, stated that improvement of egg production is still possible if appropriate selection methods are applied.

Poultry meat production is a relative new branch in agriculture, specialized meat strains were developed since 1950 (Leenstra, 1987). Because of emphasis on growth rate, the trait has improved considerably (Leenstra, 1987). Now emphasis should be put on feed conversion ratio to reduce fatness (Leenstra, 1987). There is no evidence of exhaustion of genetic variance in broilers (King, 1981).

Number of offspring per parent can be large in poultry which facilitates intense selection. The average generation interval is relatively short, about one year. This combination of factors implies that number of sires used per year should be chosen carefully. Too intense selection will considerably diminish possibilities for further selection. Optimal number of sires will depend on the selection method followed and on heritabilities of traits under selection. Both will differ between traits and between strains.

Because of relative large family sizes, within-family selection will yield good responses in poultry, simultaneously limiting rate of increase in F.

4.2 Sheep and goats

Farming of sheep and goats is characteristically distributed in the more difficult agricultural environments, which implies that these species are usually less intensively farmed relative to dairy cattle, pigs and poultry (Nicoll et al., 1986). To improve economic benefits of sheep and goat breeding, open nucleus breeding schemes (James, 1977) have been widely promoted in Australia and New Zealand (Nicoll et al., 1986). In The Netherlands synthetic breeds with a higher prolificacy than the predominant Texel breed recently were developed (Bekedam, 1986; Visscher, 1987). Proper use of these synthetics could be made by means of a nucleus structure. Within the nucleus, mating groups could be formed according to genetic relationships of rams and ewes. Rams should not be used longer than one mating season and mating groups, therefore, need to be rearranged every mating season. Such a system is preferable over circular mating in which ewes are divided over subgroups according to their pedigree and age because size of these subgroups often becomes too small for effective selection and because the generation interval is prolonged with circular mating due to the use of sires of different age classes. A fast turn-over of rams limits the rate of increase in F and has a positive effect on selection response.

4.3 Horses

Number of horses has decreased worldwide over the last decades (Langlois et al., 1983). Many breeds of horses are small populations (Flade and Skrilecz, 1971; Bohlin and Rönningen, 1975; Fehlings et al., 1983; Macluer et al., 1983; Vangen 1983). Two opposite trends are often observed: a regular decrease in number of draught horses and a constant increase in number of blood horses (Langlois et al., 1983). For the first category, main aim of the breeders often is to maintain the breed as such. Selection criteria often are not well defined (Langlois et al., 1983; Vangen, 1983) and some of the selection policy could easily be directed at conservation of genetic variance (Vangen, 1983). If pedigree information is available, additive genetic relationships between animals can be calculated and recommendations about mating combinations can be given. Number of stallions available for mating should be large enough to enable avoidance of mating of relatives and at least 20 to 30 stallions should be used per generation. It is important that length of time a stallion is used for breeding is relatively short and that he is replaced by a son.

In race horses, individual performance is of great economic importance and a development of specialized lines for different competitive activities might be necessary (Langlois et al., 1983). In such a situation, the same genetic principles as in a swine nucleus herd apply, despite the longer generation interval in horses. Intense selection for a clearly defined breeding objective is to be recommended. A breeding program, however, should not be based on a single famous Derby-winner, but should instead promote use a number of proven stallions for breeding.

4.4 Dairy cattle

Van Vleck (1986) stated that genetic gain obtained in dairy cattle was less than expected from theory because of an unnecessary long generation interval, emphasis on secondary traits and weakness in genetic evaluation of cows and bulls. He did not consider the effect of selection on the variance, which is a fourth cause of discrepancy between expected and realized genetic gain.

Short-term selection theory does not take account of the effect of selection on the variance and suggests a supremacy of alternatives in which a few highly selected animals are used for breeding (e.g. Skjervold and Langholz, 1964; Nicholas and Smith, 1983). This supremacy is overestimated. Moreover, use of just few highly selected bull-sires will lead to a fast increase in F, which affects not only the mean but also the additive genetic variance available for selection. Studies on optimal breeding programmes for dairy cattle (Skjervold and Langholz, 1964; Lindhé, 1968; Brascamp, 1975) made an approximate correction for the effect of F on the mean but ignored effects of inbreeding and selection on the additive genetic variance. These shortcomings led to an overestimation of possible genetic gain and secondly, wrongly suggest that alternatives with the most intense selection are optimal.

In dairy cattle, progeny testing is applied and BLUP procedures are used in estimation of breeding values. As a result, accuracy of selection is relatively high and, probably, use of 20 to 30 bull-sires per generation would be optimal. Number to be used annually depends on the generation interval. In a conventional progeny testing scheme, the average generation interval is six to seven years (Nicholas and Smith, 1983). With the assumption that bull-sires are used for only one year, three to five bull-sires should be used annually.

Nicholas (1979) and Nicholas and Smith (1983) argued that with multiple ovulation and embryo transfer (MOET) the generation interval could be reduced to two years if one year old females were used for embryo transfer (juvenile scheme) and to four years if females that completed one lactation were used (adult scheme). Optimal number of bull-sires used annually would simultaneously increase to about six for the adult scheme and to about 12 for the juvenile scheme. This number is larger than in the proposed MOET scheme of Nicholas and Smith (1983), which means that the expected 30 percent extra gain of MOET relative to a conventional progeny testing scheme is overestimated. With MOET, cattle breeding becomes more like pig breeding. Enlargement of number of donors from 64 (Nicholas and Smith, 1983) to 100 would, therefore, be profitable from a genetic point of view (De Roo, 1987a). Number of embryo transfers required would then become quite high, which would make the scheme costly. Further investigations towards costs and benefits of MOET are necessary.

Nicholas and Smith (1983) also considered cloning and stated that high rates of genetic improvement would be possible if this technique would become operational. A large genetic jump would indeed be possible because the population mean could be lifted to the level of the best proven bulls and bull dams. It is questionable, however, whether further genetic improvement would still be possible because of the large reduction in genetic variance which would be caused by cloning.

Burnside (1974) stated that the best proven bulls should be used maximally and was prepared to accept a longer generation interval for the sake of a stronger selection among young bulls. Present results indicate that this extra selection is not as beneficial as suggested by short-term selection theory, especially not when it causes a lengthening of the generation interval. Proven bulls, however, should be used intensely. In an optimal breeding scheme, number of proven bulls only should be larger than number of bull-sires if these bull-sires are not able to perform all the necessary inseminations. Turn-over of sires should be fast in such a scheme. In an optimal scheme, a maximum total number of inseminations per bull should be defined. Choice of such a maximum is arbitrary but a life-total equal to 20 percent of the yearly number of inseminations in the population is reasonable. This means that this maximum is lower for a small cattle breed like the Groninger Blaarkop than for the MRIJ breed (both Dutch). The maximum could be quite high for the Dutch Friesian because of the large immigration of genes from other Friesian populations.

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SUMMARY

Size of a population in genetic terms is a function of number of male and female individuals used for breeding over a generation. A breed can be small because of a small total number of individuals but also because of a small number of individuals of one sex. According to this definition, many breeds of livestock, pets and zoo animals are small populations.

Breeding scheme designed for finite populations sometimes primarily aim at conservation of animal genetic resources. In most cases, however, the breeding program should lead to continuous genetic improvement over a period of time of interest to breeders. Available additive genetic variance, therefore, should be used efficiently. This is not straightforward because selection in one generation affects the additive genetic variance in the next generation. A second complication is the increase in additive genetic relationship between animals, which is inevitable in a finite population. Inbreeding reduces additive genetic variance available for selection and, secondly, has a negative effect on the mean of traits subject to dominance.

The aim of this thesis was optimization of breeding schemes in finite populations. Attention was focussed on breeding schemes in a closed swine herd as an example of a finite population in which selection and inbreeding are both relevant. The outcome of a breeding scheme for such a herd is affected by many factors as, for example, population size and structure, founder population size and selection and mating strategies. Effects of variation in a number of these factors on selection response and rate of increase in inbreeding coefficient (F) were studied.

The genetic model used was highlighted in the first chapter. This model applied to quantitative traits and assumed that many loci of small effect each affected a trait. To prevent confounding of effects of inbreeding on the additive genetic variance and on the mean, an additive genetic model was used in chapters 3 to 5. Effects of inbreeding depression were considered in chapter 6.

A stochastic model of a closed swine herd was described in chapter 2. This model measured genetic changes in production and reproduction traits and F over a period of 25 years. Growth rate (23 to 100 kg), feed intake, lean percentage, litter size and interval from weaning to oestrus were

incorporated in the model because of their economic relevance to pig breeding. The model included overlapping generations, continuous mating and farrowing and weekly selection of boars and sows. Week was the unit of time. This model was used in subsequent chapters. The parameters used applied to a sire line.

Population size at the nucleus level is an important factor with respect to costs and benefits of pig breeding. Selection response is dependent on number of boars and of sows available for selection and on number of each sex used for breeding. Effects of variation in population size and in intensities of selection on selection response and rate of increase in F were reported in chapter 3. Results were compared to expectations from selection theory and from theory of effective population size.

Advantages of intense selection in short-term response were less than expected because assumptions of independent observations and constant variance were violated. Selection induced linkage disequilibrium and reduced the additive genetic variance. Intensity of selection was reduced because of small numbers of families. Comparison of alternative breeding schemes should include a correction for the amount of linkage disequilibrium caused by each breeding scheme. The equilibrium additive genetic variance should be used in the calculation of expected response to selection. When number of families is small, as in many practical situations, selection intensities used should also be corrected for family size, except when available family information is included in the index and selection intensities are based on number of families.

Response was curvilinear with time, and curvilinearity increased with intensity of selection. Increased relationships between animals caused reduced variance available for selection and diminished response. When the time period included in the evaluation of breeding schemes increased, optimal annual number of boars also increased.

Equations were derived to describe cumulative response in year 25 as a function of size of the sow herd and annual number of boars. With 25, 50, 100 and 150 sows, 52, 66, 75 and 84 percent of maximum response with an infinite number of sows was attained. Optimal annual number of boars depended on size of the sow herd: when herd size increased, optimal annual number of boars increased to 15.

Drift caused considerable differences in response between replicates. These differences, however, were small compared to differences in means between sow alternatives. Splitting of a line into independent sublines, therefore, is unadvisable because of reduced expected response due to smaller population size.

The design of a mating system for selected animals needs special attention. Mating policy includes the choice whether and to what extent mating of relatives should be avoided. It also implies choice of number of boars to be used simultaneously for breeding. In chapter 4 alternative mating policies were compared.

Under the additive genetic model followed, cumulative response over a period of 25 years was generally highest with 3 boars used simultaneously and no avoidance of mating of relatives. With avoidance of mating of relatives, number of offspring of sires with few relatives was increased. These sires probably were not as good genetically as sires with many relatives, because selection was on phenotype alone. With avoidance of mating of relatives breeding values of mates will be more diverse and the additive genetic variance among offspring will be less than without avoidance of mating of relatives. Unequal numbers of offspring of sires also contributed to a lower additive genetic variance and, thus, to a lower response to selection for alternatives with avoidance of mating of relatives. It should be noted that inbreeding depression was not a consideration in this chapter.

Avoiding mating of relatives initially postponed the increase of F. Rate of increase in F after year five, however, was rather independent of mating policy. Differences in F in year 25 between alternatives with and without avoidance of mating of relatives were considerable and ranged from 2.1 percent for 100 sows, 20 boars annually and 10 boars at a time to 6.9 percent for 100 sows, 5 boars annually and 3 boars at a time. The risk of an unexpected high level of F was also higher when there was no avoidance of mating of relatives. A mating system with avoidance of mating of close relatives only probably is optimal.

At the start of a new line, the question of size of the founder population arises. The founder population should have a high mean breeding value and contain a substantial amount of genetic variation. Effects of changes in size of the founder population, in effective population size after the foundation period and in intensity of selection of founder animals from a base population were evaluated in chapter 5.

Determination of optimal size of the founder population implies a balancing of mean breeding value and additive genetic variance in the founder group. Optimal number of founder animals depends on differences in estimated breeding values between animals, on the accuracy of these estimates and on the risk of low response a breeder is willing to take. This risk increases at a decreasing number of founder animals.

Use of five founder boars provided, on average, good responses. The established level of additive genetic variance offered good possibilities for further selection and fast reduction of this variance in the early years of the breeding program was prevented.

Optimal number of founder sows depended on desired size of the herd. A gradual increase of number of sows towards the desired size of the herd was optimal. This strategy implies culling of sows with a low performance, even if the desired size of the herd is not reached yet. Selection of sows should be mild, because build up of the sow herd should be done reasonably fast. A herd of 100 sows could be founded acceptably by 25 founder sows.

Effects of a temporary restriction of population size on selection response depend on number and genetic relationships of remaining animals. A fast increase in effective population size after such a bottleneck can limit the rate of increase in F and the negative effects on response.

The level of F is relevant to breeders because it affects the additive genetic variance. Direct inbreeding depression effects on production traits are less important in a sire line because a loss in heterozygosity will be regained in hybrid slaughter animals. Inbreeding depression, however, might also affect selection response indirectly. Through its effect on fertility, inbreeding depression will affect number of animals available for selection and, thus, selection response. Effects of inbreeding depression were investigated in chapter 6.

Three sets of partial regression coefficients of F on litter size at birth and at weaning and on growth rate were considered: no inbreeding depression, a set based on literature and a set of values twice as large as indicated by literature. Two sizes of the sow herd were considered, 25 and 100, and annual number of boars varied from 5 to 20.

Inbreeding depression induced a negative correlation between performance and F and, therefore, slightly diminished rate of increase in F when animals available for selection differed in F. Mild selection for litter size improved breeding values and, simultaneously, limited inbreeding depression for the trait. Selection counteracted inbreeding depression most effectively with a low rate of increase in F.

Inbreeding depression affected response for production traits most through its effect on the mean. Reduction in litter size had a limited effect on intensity of selection, because only two boars per litter were tested. This effect might be larger with other testing strategies or less prolific species. Response was reduced when animals available for selection differed in F, because of a bias in estimated breeding values. Data to be used in estimation of breeding values, therefore, should be corrected for differences in F between animals.

Optimal annual number of boars was largely unaffected by degree of inbreeding depression. The main effect of inbreeding depression was to reduce response of alternatives with five boars annually relative to other boar alternatives. Even without inbreeding depression, number of boars used annually should be larger than five.

Effects of opening of the nucleus and breeding programmes that aim at conservation of animal genetic resources were considered in chapter 7. Implications of the study for the design of breeding schemes in general and, more specific, for selection in some livestock species were also discussed.

Introduction of new breeding animals from outside the nucleus is only worthwhile occasionally. The effect on selection response and F will be limited and the selection policy followed in the nucleus will be of major importance to the benefits of the breeding scheme.

With maintenance of genetic variance as the main objective of breeding, emphasis should be on limiting the rate of increase in F. Differences in contributions of animals to the next generation of offspring should be minimized. Use of within-family selection, therefore, is advisable. Number of sires and dams used per generation should be as equal as possible. This can be realized at relatively low costs by a fast turn-over of sires and a long herd life of dams.

Many populations of livestock are small in genetic terms because effective number of sires is small. With differential numbers of matings per sire, effective number of sires is considerably smaller than actual number of sires. Use of a very small number of sires will limit genetic improvement and will cause a high rate of increase in F. Optimization of breeding schemes not only implies intense selection of breeding stock but also includes use of a sufficient number of sires to insure continuous genetic improvement over the period of time of interest to breeders.

SAMENVATTING

De omvang van een populatie in genetische zin wordt bepaald door het aantal mannelijke en vrouwelijke dieren dat per generatie voor de fokkerij wordt gebruikt. Een populatie kan klein zijn omdat het totale aantal dieren in de populatie klein is, maar ook omdat het aantal dieren van één sexe klein is. Veel populaties van landbouwhuisdieren, gewone huisdieren en dierentuindieren zijn in genetische zin dan ook kleine populaties.

In een aantal gevallen heeft het fokprogramma voor zo'n kleine populatie alleen tot doel om de soort in stand te houden. Meestal wordt echter van het fokprogramma verwacht dat het leidt tot een voortdurende genetische verbetering van de primaire en secundaire produktie-eigenschappen van een ras. Die vooruitgang dient zo groot mogelijk te zijn in de periode die voor fokkers economisch van belang is. Dit betekent dat optimaal gebruik gemaakt moet worden van de genetische variatie die beschikbaar is in de populatie. Dit is niet eenvoudig, omdat selectie in de ene generatie de genetische variabiliteit in de volgende generatie beïnvloedt. Een tweede probleem is de toename in verwantschap tussen dieren, die onvermijdelijk is in kleine populaties en leidt tot het paren van verwanten ("inteelt"). Inteelt veroorzaakt een afname van de genetische variantie. Wanneer dominantie een rol speelt bij de vererving van een kenmerk, zal inteelt bovendien leiden tot een afname van het gemiddelde prestatieniveau (inteeltdepressie).

Doel van dit proefschrift was het optimaliseren van fokprogramma's voor kleine populaties. De aandacht was geconcentreerd op het fokbeleid voor een gesloten varkensbedrijf, aangezien dit een voorbeeld is van een kleine populatie, waarin zowel selectie als inteelttoename belangrijk zijn. De fokresultaten op een dergelijk bedrijf worden door veel factoren beïnvloed. Enkele daarvan zijn: de populatie-omvang en -structuur, de omvang van de uitgangspopulatie en de toe te passen selectie- en paringsstrategie. Effecten van variatie in een aantal van deze factoren op de fokresultaten en de inteelttoename zijn onderzocht.

In het zogenaamde genetische model wordt vastgelegd hoe de genetische waarde van een individu, het genotype, tot stand komt. Het gebruikte genetische model is toegelicht in hoofdstuk 1. Dit model geldt voor kwantitatieve kenmerken. Aangenomen is dat deze kenmerken worden beïnvloed door veel genen, die elk een klein effect hebben. Om verstrengeling van de effecten van inteelt op de genetische variantie en op het gemiddelde te voorkomen, is een additief genetisch model gebruikt in de hoofdstukken 3 tot en met 5. Inteeltdepressie is bestudeerd in hoofdstuk 6.

In hoofdstuk 2 is een stochastisch model van een gesloten varkensbedrijf beschreven. Dit model bepaalde zowel de inteelttoename als genetische veranderingen in produktie- en reproduktiekenmerken in de loop van 25 jaar. Groei per dag, voeropname, vleespercentage, worpgrootte en het interval spenen-bronst werden in het model opgenomen vanwege hun economisch belang voor de fokkerij. Het model hield rekening met overlappende generaties en met het feit dat dekken, werpen en selectie van zeugen en beren in de praktijk continue processen zijn. De week diende als tijdseenheid. Dit model is in de volgende hoofdstukken toegepast. De gebruikte parameters representeren de situatie van een berenlijn.

De populatieomvang in de topfokkerij is belangrijk voor zowel kosten als opbrengsten van het fokprogramma. Het fokresultaat hangt af van het aantal beren en zeugen dat beschikbaar is voor selectie en van het aantal dieren van elke sexe dat voor de fokkerij gebruikt wordt. Effecten van variatie in populatie-omvang en in selectiescherpte op het fokresultaat en de inteelttoename zijn beschreven in hoofdstuk 3. Resultaten zijn vergeleken met verwachtingen, gebaseerd op selectietheorie en op theorie van effectieve populatie-omvang.

Voordelen van strenge selectie met betrekking tot het fokresultaat in de eerste jaren van selectie waren kleiner dan verwacht. Selectie blijkt het koppelingsevenwicht tussen loci, dat aanwezig is bij random mating, te verstoren. Dit zogenaamde linkage disequilibrium betekent een afname van de voor selectie beschikbare genetische variantie. Daarnaast zorgt een gebruik van slechts enkele vaderdieren ervoor, dat de waarnemingen waarop selectie gebaseerd is niet langer ongecorreleerd zijn. De selectie-intensiteit is daardoor kleiner dan op grond van het aantal voor selectie beschikbare dieren zou worden verwacht. Bij de vergelijking van alternatieve fokprogramma's moet daarom rekening worden gehouden met de mate van linkage disequilibrium die veroorzaakt wordt door elk van deze fokprogramma's. Wanneer het aantal families klein is, zoals vaak het geval is in de praktijk, moet bij het bepalen van de selectie-intensiteit rekening worden gehouden met de familiestructuur. Dit kan achterwege blijven als alle beschikbare familieinformatie wordt gebruikt in de indexberekeningen en als de selectie-intensiteit wordt afgeleid van het aantal families.

Het fokresultaat, uitgezet tegen de tijd, vertoonde een curvilineair verloop. De kromming van de responscurve nam toe wanneer de intensiteit van selectie toenam. De toenemende verwantschap tussen dieren zorgde voor een afname in de genetische variantie en leidde op die manier tot een afname in de genetische vooruitgang per jaar. Het optimale aantal per jaar in te zetten beren nam toe wanneer het aantal jaren, dat in de evaluatie van fokprogramma's werd betrokken, toenam.

Er zijn vergelijkingen ontwikkeld, waarmee de genetische vooruitgang in 25 jaar kon worden beschreven als een functie van de omvang van de zeugenstapel en het aantal per jaar gebruikte beren. De genetische vooruitgang, die kon worden behaald met 25, 50, 100 en 150 zeugen, was 52, 66, 75 en 84 procent van de theoretisch maximaal haalbare genetische vooruitgang met een oneindig grote zeugenstapel. Het optimale aantal per jaar te gebruiken beren was afhankelijk van de omvang van de zeugenstapel. Wanneer het aantal zeugen toenam, nam het optimale aantal beren toe tot 15.

Drift zorgde voor behoorlijke verschillen in fokresultaat tussen herhaalde waarnemingen met dezelfde fokkerijstrategie. Deze verschillen waren echter klein in vergelijking met de verschillen in gemiddelde fokresultaten tussen alternatieven met een verschillend aantal zeugen. Dit betekent dat het opsplitsen van een lijn in een aantal onafhankelijke sublijnen niet is aan te raden, omdat het waarschijnlijk zal leiden tot een slechter fokresultaat.

Het ontwerpen van een paringssysteem voor geselecteerde dieren verdient speciale aandacht. Dit houdt in dat een keuze moet worden gemaakt of en in welke mate het paren van verwante dieren moet worden vermeden. Het vergt ook een keuze van het aantal beren dat tegelijkertijd voor de fokkerij moet worden gebruikt. In hoofdstuk 4 zijn alternatieve paringssystemen vergeleken.

Bij het gebruikte additief genetische model was de genetische vooruitgang in 25 jaar in het algemeen het grootst, wanneer 3 beren tegelijkertijd werden ingezet voor de fokkerij en wanneer geen vermijding van het paren van verwanten werd toegepast. Het vermijden van het paren van verwanten leidde tot meer nakomelingen voor beren met weinig verwanten. Deze beren waren waarschijnlijk genetisch minder goed dan beren met veel verwanten, omdat alleen geselecteerd werd op eigen prestatie. Bij het vermijden van het paren van verwanten waren de fokwaardes van dieren die werden gepaard gemiddeld meer verschillend dan zonder inteeltvermijding het geval was. Inteeltvermijding zorgde op die manier voor een relatief kleinere genetische variatie in de nakomelingen. Ongelijke aantallen nakomelingen per beer droegen ook bij aan een kleinere genetische variantie en een minder goed fokresultaat in het geval van inteeltvermijding. Opgemerkt moet worden, dat inteeltdepressie buiten beschouwing is gelaten in dit hoofdstuk.

Vermijding van het paren van verwanten zorgde voor uitstel van de inteelttoename. De inteelttoename na jaar 5 werd echter nauwelijks beïnvloed door het paringssysteem. Toch werden er behoorlijke verschillen in inteeltcoëfficiënt in jaar 25 tussen alternatieven met en zonder inteeltvermijding waargenomen; deze liepen op van 2.1 procent voor 100 zeugen, 20 beren per jaar en het gebruik van 10 beren gelijktijdig tot 6.9 procent voor 100 zeugen, 5 beren per jaar en het gebruik van 3 beren gelijktijdig. Het risico van een onverwacht hoge inteelttoename was ook hoger wanneer geen inteeltvermijding werd toegepast. Een paringssysteem waarbij alleen het paren van nauwe verwanten wordt voorkomen is wellicht optimaal.

Bij de vorming van een nieuwe lijn is de vraag naar het aantal dieren, waarmee die nieuwe lijn moet worden begonnen, cruciaal. De gemiddelde genetische aanleg van de uitgangspopulatie dient goed te zijn en bovendien moet er een behoorlijke genetische variatie aanwezig zijn. Effecten van variatie in omvang van de uitgangspopulatie, in effectieve populatie-omvang na de beginperiode en in selectie-intensiteit, waarmee de uitgangspopulatie wordt geselecteerd uit een basispopulatie, zijn bestudeerd in hoofdstuk 5.

Het bepalen van de optimale omvang van de uitgangspopulatie betekent het in evenwicht brengen van de gemiddelde fokwaarde en de genetische variatie in die populatie. Het optimale aantal dieren in de uitgangspopulatie hangt af van de verschillen in geschatte fokwaarde tussen dieren, van de nauwkeurigheid van deze schattingen en van het risico van een slecht fokresultaat, dat een fokker bereid is te nemen. Dit risico neemt toe met een afnemend aantal uitgangsdieren.

Het gebruik van vijf beren als stamvader gaf in het algemeen goede fokresultaten. Het ontstane niveau van genetische variatie bood goede mogelijkheden voor verdere selectie, terwijl een snelle achteruitgang van de genetische variatie in de beginjaren van het fokprogramma werd voorkomen.

Het optimale aantal stammoeders was afhankelijk van de gewenste omvang van de zeugenstapel. Een geleidelijke toename van het aantal zeugen tot het gewenste aantal was optimaal. Dit betekent dat slechte zeugen moeten worden opgeruimd, ook als de gewenste omvang van de zeugenstapel nog niet bereikt is. Die selectie mag niet te scherp zijn, omdat het belangrijk is dat de gewenste omvang van de zeugenstapel snel bereikt wordt. Een lijn van 100 zeugen kon, uitgaande van 25 stammoeders, op een acceptabele manier worden opgebouwd.

De gevolgen van een tijdelijke beperking van de populatieomvang hangen af van het aantal overblijvende dieren en van de mate waarin die dieren verwant zijn. Het snel uitbreiden van de effectieve populatiegrootte na zo'n bottleneck kan zowel de inteelttoename als de negatieve gevolgen voor het fokresultaat beperken.

Inteelttoename is van belang voor de fokkerij, omdat het de genetische variantie beïnvloedt. Directe inteeltdepressie-effecten op produktiekenmerken zijn in een berenlijn minder belangrijk, omdat een verlies in heterozygotie zal worden teruggewonnen in hybride slachtdieren. Inteeltdepressie kan het fokresultaat echter ook indirect beïnvloeden. Via een effect op vruchtbaarheid zal inteeltdepressie het aantal voor selectie beschikbare dieren en daarmee ook het fokresultaat beïnvloeden. Inteeltdepressie-effecten zijn onderzocht in hoofdstuk 6.

Effecten van inteeltdepressie op worpgrootte bij de geboorte en bij het spenen en op groeisnelheid zijn bestudeerd. Hierbij zijn drie niveau's van inteeltdepressie onderscheiden: geen inteeltdepressie, een niveau dat in overeenstemming was met in de literatuur gevonden waardes en een niveau dat twee keer zo hoog lag, als door de literatuur werd aangegeven. Zeugenstapels met 25 en 100 zeugen zijn bekeken, waarbij het aantal per jaar gebruikte beren varieerde van 5 tot 20.

Inteeltdepressie veroorzaakte een negatieve correlatie tussen prestatieniveau en de inteeltcoëfficiënt (F) en zorgde daarom voor een kleine vermindering van de inteelttoename wanneer de voor selectie beschikbare dieren verschilden in F. Er was een geringe selectiedruk op worpgrootte. Dit zorgde voor een verbetering van de erfelijke aanleg voor dit kenmerk en beperkte tegelijkertijd de grootte van de inteeltdepressie. Dit effect was het sterkst wanneer F langzaam toenam.

Inteeltdepressie beïnvloedde de genetische vooruitgang voor produktiekenmerken het meest door het effect op het gemiddelde. De achteruitgang in worpgrootte had maar een beperkt effect op de selectie-intensiteit, omdat slechts twee beren per worp werden getest. Dit effect zou groter kunnen zijn bij een andere teststrategie of bij minder vruchtbare diersoorten. De genetische vooruitgang nam af wanneer voor selectie beschikbare dieren verschilden in F. Gegevens die worden gebruikt voor het schatten van fokwaardes, moeten daarom gecorrigeerd worden voor verschillen in F tussen dieren.

Het optimale aantal per jaar te gebruiken beren werd nauwelijks beïnvloed door het niveau van inteeltdepressie. Het belangrijkste gevolg van inteeltdepressie was de relatieve vermindering van het fokresultaat voor alternatieven met vijf beren per jaar ten opzichte van andere beeralternatieven. Ook zonder inteeltdepressie moet het aantal per jaar gebruikte beren groter zijn dan vijf.

Effecten van het introduceren van nieuw fokmateriaal op het topfokbedrijf en fokprogramma's, die primair het in stand houden van bepaalde diersoorten ten doel hebben, zijn besproken in hoofdstuk 7. Gevolgen van dit onderzoek voor het ontwerpen van fokprogramma's in het algemeen en voor selectie in een aantal soorten landbouwhuisdieren in het bijzonder, zijn ook besproken in dat hoofdstuk.

Het introduceren van nieuw fokmateriaal in de topfok is slechts in weinig situaties foktechnisch interessant. Het effect van een dergelijke import op het fokresultaat en de inteelttoename zal beperkt zijn, terwijl het fokresultaat voornamelijk zal afhangen van het in de topfok gevolgde fokbeleid.

Wanneer het in stand houden van de genetische variatie de belangrijkste doelstelling van het fokbeleid is, moet de nadruk liggen op het beperken van de inteelttoename. De verschillen in aantallen nakomelingen van fokdieren dienen zo klein mogelijk te zijn. Binnen-familie selectie is daarom een aan te raden selectiemethode. Het aantal mannelijke en vrouwelijke dieren, dat per generatie voor de fokkerij gebruikt wordt, moet zo gelijk mogelijk zijn. Dit kan worden gerealiseerd tegen relatief lage kosten door mannetjes slechts kort te gebruiken en door vrouwtjes juist een lang leven te gunnen.

Veel populaties van landbouwhuisdieren zijn klein in genetische zin, omdat het effectieve aantal mannelijke dieren klein is. Wanneer er grote verschillen zijn in aantallen nakomelingen per mannetje, is het effectieve aantal mannelijke dieren behoorlijk kleiner dan het werkelijke aantal. Gebruik van slechts enkele mannelijke dieren zal de genetische vooruitgang beperken en zal bovendien zorgen voor een snelle inteelttoename. Optimalisatie van fokprogramma's betekent niet alleen het streng selecteren van in te zetten fokmateriaal, maar ook het gebruiken van een toereikend aantal mannelijke dieren om een voortdurende genetische vooruitgang, in de periode die van economisch belang is voor de fokkers, te verzekeren.

Curriculum vitae

George de Roo werd op 17 april 1959 geboren te Sellingen (Groningen). Hij bezocht de christelijke scholengemeenschap "Jan van Arkel" te Hardenberg en behaalde het Atheneum diploma in 1977. In september van dat jaar begon hij aan de studie Zoötechniek aan de Landbouwhogeschool te Wageningen. Deze studie werd in maart 1983 met lof afgesloten. Het doctoraal examen omvatte Veeteelt als hoofdvak en Ethologie, Informatica, Algemene Agrarische Economie en Internationale Betrekkingen en Ontwikkelingen als bijvakken. In april 1983 trad hij als wetenschappelijk assistent in dienst van de vakgroep Veefokkerij van de Landbouwhogeschool. Hij werkte een half jaar aan een onderzoeksproject op het gebied van exterieur van varkens en begon in december 1983 met het in dit proefschrift beschreven onderzoek. Sinds 1 januari 1988 is de auteur werkzaam bij de firma Lavecom te Arnhem en houdt zich daar als systeemanalist/landbouwkundige bezig met vraagstukken op het gebied van de agrarische automatisering.