MATERNAL AND GENETIC INFLUENCES ON PRODUCTION AND REPRODUCTION TRAITS IN PIGS

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MATERNAL AND GENETIC INFLUENCES ON PRODUCTION AND REPRODUCTION TRAITS IN PIGS

Proefschrift
ter verkrijging van de graad van
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dr. C.C. Oosterlee,
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in het openbaar te verdedigen
op vrijdag 15 april 1983
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen

STELLINGEN

I

Het opgroeien van een gelt in een grote toom leidt tot een negatieve milieuinvloed tot uitdrukking komend in een kleinere eerste worp.

Dit proefschrift.

II

Ten onrechte wordt in de literatuur geconcludeerd dat bij een door maternale invloeden veroorzaakte negatieve dochter-moeder regressie-coëfficiënt voor worpgrootte, het selecteren van geltjes uit de grootste tomen geen genetische vooruitgang oplevert.

Rutledge, J.J., 1980. Fraternity size and swine reproduction. J.Anim. Sci., 16: 259-266.
Robison, O.W., 1981. The influence of maternal effects on the efficiency of selection: a review.
Livest. Prod. Sci. 8: 121-137.
Dit proefschrift.

III

De post-natale maternale invloed, voor zover bepaald door de worpgrootte tijdens de zoogperiode, veroorzaakt een verlaging van de regressiecoëfficiënt van fokwaarde op fenotypische waarde. De daaraan gekoppelde verlaging van de respons van selectie op worpgrootte bij varkens is verwaarloosbaar.

Dit proefschrift.

IV

De positieve relatie tussen groei en melkconsumptie in tomen van 12 geeft aan dat naast het aantal spenen ook de melkproduktie van de zeug een beperkende factor gaat vormen voor de groei van biggen.

V

Het negatieve effect van selectie tegen halothaanovergevoeligheid op produktiekenmerken wordt voor een groot deel gecompenseerd door een toename van de worpgrootte.

VI

Verbetering van de bedrijfsprestatietoets en het bestaan van genotype-milieu interacties zal het belang van praktijkgegevens voor de fokwaardeschatting van beren doen toenemen.

VII

De kracht en zwakte van het varkensstamboek is gelegen in de populatieomvang van respectievelijk varkens en fokkers.

VIII

Het nut van een proefstation voor de varkenshouderij is meer gelegen in het vertalen van onderzoeksresultaten naar de praktijk toe dan in het uitvoeren van proeven.

IX

De noodzakelijke verbetering van het fokkerijbeleid bij paardenstamboeken mag niet leiden tot schaalvergroting.

X

Het niet in een vroeg stadium dwingend verwijzen van studenten naar een voor hen geschiktere opleiding leidt tot verspilling en is a-sociaal.

XI

Het op een correcte manier beoordelen van onderzoeksprojecten in sectorale onderzoekscommissies is even moeilijk als het voeren van een geloofwaardige politiek.

XII

Studentenstops: de één zijn dood, de ander zijn brood.

XIII

Struisvogelpolitiek steekt meer de kop op naarmate de problemen toenemen.

H.A.M. van der Steen
Maternal and genetic influences on production and reproduction traits in pigs.
Wageningen, 15 april 1983.

aan Tini
aan Vader en Moeder

Steen, H.A.M. van der, 1983. Maternal and genetic influences on production and reproduction traits in pigs (Maternale en genetische invloeden op produktie en reproduktie kenmerken bij varkens).
Department of Animal Breeding of the Agricultural University, Wageningen, The Netherlands.
Also: Doctoral thesis, Wageningen

VOORWOORD

Het in dit proefschrift beschreven onderzoek is uitgevoerd bij de vakgroep Veefokkerij van de Landbouwhogeschool te Wageningen.

Een onderzoek als het beschrevene kan alleen worden uitgevoerd met hulp en steun van velen. De uitvoering van het onderzoek vergde vier jaren. Een verstoring door de uitbraak van ziekten, onvoldoende zorgvuldige planning of menselijke fouten is dan ook niet denkbeeldig. Inzet van betrokkenen en een dosis geluk hebben er voor gezorgd dat de proef zonder essentiële storingen is uitgevoerd.

Mijn promotor, prof.dr.ir. R.D. Politiek heeft de aanzet tot dit type onderzoek gegeven. Ik dank hem oprecht hartelijk voor zijn stimulerende belangstelling, de geboden mogelijkheden en inbreng bij discussies.

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C.J. Bol heeft op adequate wijze het simulatieprogramma geschreven.

Het typewerk is op accurate wijze uitgevoerd door mw. P.E. l'Amie-van Eden, mw. E.T. van Beek-Geurtsen, mw. G.L.M. Leenarts-Wiggerman en mw. J.G.J.M. Stijnman-Mulder.

De heer W. Heye heeft de figuren nauwgezet getekend.

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1 INTRODUCTION

The profitability of pig production may be expressed as a function of reproductivity and productivity (Moav, 1966). The optimal selection pressure on reproductivity relative to productivity depends on the economic value of the expected response to selection. Reproductive performance is primarily a function of the dam and involves age at first oestrus, conception rate, litter size and the interval between weaning and oestrus.

An increase of the litter size would improve the reproductive performance. In spite of this, litter size has been rather stable in most countries over the last decades (Skjervold, 1979; C.A.D.V., 1980; Johansson, 1981). This may have been caused by a lack of, or no response to, selection for litter size, a deterioration in the environment or negative effects of selection for production characteristics. One might ask whether selection for litter size is worthwhile. The heritability of the trait, possible selection differential and economic value of litter size are important. Of these, heritability seems to be the major limiting factor. Estimates have been consistently low ($\sim$0.10). This may be due to (Skjervold, 1979):

- small additive genetic variance
- excessive environmental variability
- negative correlations between direct genetic and maternal effects
- negative genetic correlations between components of the trait.

Some 25 years ago, Falconer (1955, 1960) reported that mice reared in large litters were smaller at 6 weeks of age and produced smaller litters as dams. The existence of a negative maternal effect on litter size will of course result in a significant reduction in the selection response (Skjervold, 1979). Rutledge (1980) concluded that selection of replacement gilts born and reared in large litters would not bring about desirable genetic changes in litter size. These conclusions were based on the fact that a negative correlation between direct genetic and maternal effects reduces the daughter-dam regression coefficient. Consequently it affects also the heritability estimated by this method.

A large part of our knowledge of maternal effects is based on results obtained in mice. Up to now the importance of maternal effects on litter size in pigs and the genetic implications, in particular the effect on response to selection, are not fully understood. To what extent do maternal effects counterbalance the response to selection for litter size and what can be done to overcome this problem?

The objectives of this study were to determine the effect of the size of litter in which a gilt is raised on its production and reproductive characteristics and their genetic implications.

The literature is summarized in chapter 2. Materials and methods are described in chapter 3 and results in chapter 4. Attention is focussed mainly on the effect of standardization level on reproduction traits, in particular the size of the first litter. Results are discussed in chapter 5. Genetic implications of maternal effects are discussed on the basis of a simulation study and a theoretical derivation of the influence of maternal effects on the response to selection for litter size.

2 LITERATURE

The main purpose of this section is to summarize the results reported in the literature of maternal and genetic influences upon reproduction traits, especially litter size of nulli- and primiparous sows.

The main topics will be
- theory of maternal effects
- heritability estimated by daughter-dam regression, granddaughter-granddam regression and paternal half sib analysis
- selection experiments in pigs and mice
- estimates of the maternal influence.

Some attention will be given to factors which influence the results of the experiment which are given in chapter 4.

2.1 Maternal effects

2.1.1 Definition of the maternal influence

A dam may influence her offspring through the environment she provides as well as through the genes transmitted to the offspring. This environmental effect of the dam upon her offspring is referred to as maternal influence. Several factors may be responsible for this. It may be due to the cytoplasm of the egg, the intra-uterine environment or post-natal environment, e.g. milk production and/or mothering ability (Robison, 1972). Part of this maternal influence may be genetically determined.
A dam may influence several traits of her offspring e.g. growth, behaviour, fertility. This study will be focussed on the post-natal maternal influence upon fertility of the daughter. A dam influences her offspring from birth to weaning through the environment provided to the individual offspring. Variation in litter size, milk production and mothering ability of the dam may result in variation of the maternal influence upon litters. Individual piglets experience a variable environment of which milk consumption and competition with litter mates may be important factors. Those factors may be closely linked to litter size during the suckling period.

2.1.2 Theory

2.1.2.1 Model according to Willham

Willham (1963) assumed P_x, for simplicity, to be the sum of two component characte one being influenced by the genotypic value of X and the other by the genotypic value of an individual related to X, say W. Denote the two components of the character as o and m symbolizing the offspring component and the maternal effect.

$$P_x = G_{ox} + E^*_{ox} + G_{mw} + E_{mw} \qquad (1$$

where P_x = phenotypic value of individual X
G_{ox} = direct genotypic value of individual X
E^*_{ox} = direct environmental value of individual X
G_{mw} = genotypic value of individual W as expressed in P_x
E_{mw} = environmental value of individual W as expressed in P_x.

The maternal influence may be split into a pre-natal and post-natal component.

$$G_{mw} = G_{m1,w} + G_{m2,w} \qquad (2$$
$$E_{mw} = E_{m1,w} + W_{m2,w} \qquad (3$$

Figure 2.1 illustrates such a model when W and V represent the dam and granddam respectively of X, and A's denote additive genetic values rather than genotypic values. In this figure r's denote genetic correlation coefficients and h's and e's path coefficients.

The direct environmental influence upon individual X,which is not caused by the mother,may be split into an environmental influence common to litter mates (C) and other environmental influences (E_{ox}).

$$E^*_{ox} = C + E_{ox} \qquad (4$$

Combining equations 1 to 4 gives

$$P_x = G_{ox} + G_{mw} + C + E_{ox} + E_{mw} \qquad (5$$

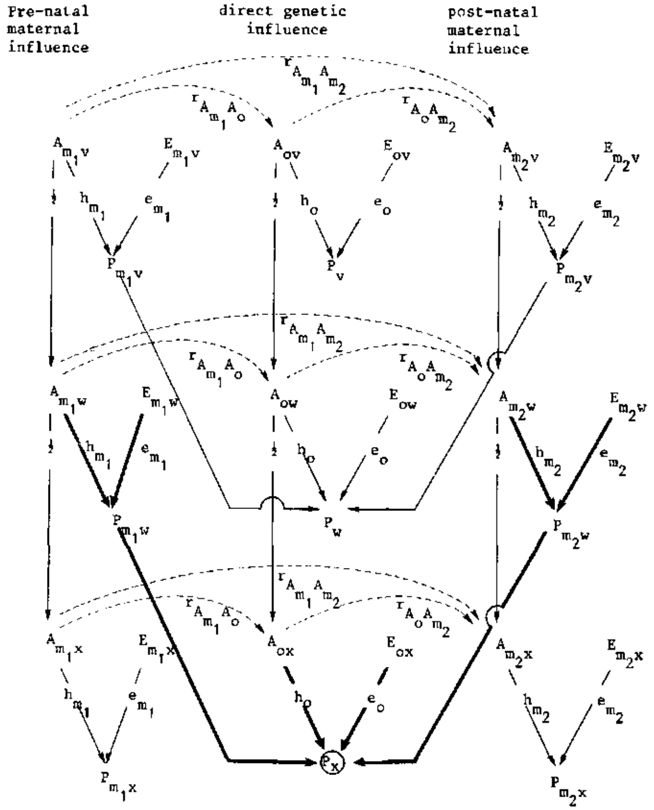

Fig. 2.1 A path coefficient diagram describing a phenotypic value influenced by a pre- and post-natal maternal effect.

2.1.2.2 Model according to Falconer

According to Falconer (1965) a maternal effect can be expressed as a deviation to be added to the other determinants of an individual's deviation from the population mean, so that the phenotypic value, P, of an individual, measured as a deviation from the population mean, can be expressed as

$$P = A + M + D + C + E \qquad (6)$$

where A = additive genetic value of an individual
M = maternal effect to which the individual is subject
D = dominance deviation

C = environmental factor common to full-sibs (litter mates) that is not included in the maternal effect.

M was defined as a linear function, m, of the mother's phenotypic value, P', measured as a deviation from the population mean, so that

$$M = mP'$$

The coefficient m is the partial regression coefficient of daughters' phenotypic values on mothers' phenotypic values in the absence of genetic variation among the mothers.

2.1.2.3 Relation between the models according to Willham and Falconer

To show the relation between the two models it is necessary to split the maternal components of equation 5 into a part related to litter size and a part not related to litter size. These are denoted by l and n respectively.

$$\begin{array}{ll} \text{Model of Falconer} & \text{Model of Willham} \\ P = A + D & P_x = G_{ox} \\ \quad + mP' & \quad + G_{ml,w} + E_{ml,w} \\ \quad + C & \quad + C + G_{mn,w} + E_{mn,w} \\ \quad + E & \quad + E_{ox} \end{array} \qquad (8)$$

The C-component in the model of Falconer includes maternal effects as far as they are not related to pre- and post-natal litter size. For instance the variation in milk consumption per piglet is caused by variation in milk production by the mother at a fixed size of the litter, a fixed feeding level and by variation in litter size The relation between litter size and milk production per piglet will not be linear and the correlation coefficient will be less than 1. So part of the post-maternal influence that is determined by milk consumption per piglet will not be related to litter size.

2.1.2.4 Heritability estimated by daughter-dam and granddaughter-granddam regression

Falconer (1965) expressed the covariance between P (size of the first litter of the daughter) and P' (size of the litter of the mother in which the daughter was born i.e. daughter's birth litter) in terms of additive genetic and phenotypic variances and m

$$\mathrm{cov}(PP') = V_A\left(\frac{1}{2-m}\right) + mV_{P'}, \quad \text{(eq.11; Falconer, 1965)} \qquad (9)$$

Negative m-values reduce this covariance and hence the daughter-dam regression coefficient.

The regression coefficients of P with P' (daughter's birth litter) and P" (dam's birth litter) were given by Alsing et al. (1980).

$$b_{PP'} = h^2 \frac{1}{2-m} + m \qquad (10)$$

and $$b_{PP''} = h^2 \frac{1 + 2m}{2^{*}(2-m)} + m^2 \qquad (11)$$

To illustrate the influence of maternal effects upon heritability estimated by daughter-dam and granddaughter-granddam regression a few simple calculations are carried out.

Suppose $V_A / V_P = 0.20$,

then h^2 estimated by: daughter-dam regression and granddaughter-granddam regression

for m = 0	are	0.200		0.200
-0.05		0.095		0.186
-0.10		-0.010		0.192
-0.15		-0.114	and	0.220 respectively.

Heritability estimates are biased downwards by maternal effects if daughter-dam regression is used, while this is not the case with granddaughter-granddam regression.

Heritability estimates are not biased by maternal effects if paternal half-sib analysis is used.

No distinction has been made in the literature between pre- and post-natal maternal effects in deriving the appropriate formulae. These derivations are given in appendix 9.

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* Alsing et al. (1980) gave a value of 4 instead of 2; a proof of the correct formula is given in appendix 9.

2.2 Heritability estimates for litter traits

2.2.1 Heritability estimates from large data sets

Heritability estimates for litter size at birth are given in table 2.1.

Table 2.1 Summary of literature on heritability of litter size.

author	method	number of daughter-dam pairs (DDR) or number of litters (PHS)	trait	overall	heritability estimate		breed
					for each parity	for a sum of litters	
Urban et al. (1966)	DDR	3119	NPT	0.09			
Eikje (1970)	PHS		NPL				
high herd level		4918		0.16			
low herd level		5938		0.12			
Legault (1970)	DDR	1735	NPL	0.11	1 0.08	1-2 0.08	LW
		1424			2 0.03	1-3 0.08	
		1057			3 0.15		
		689			4 0.22		
		993			≥5 0.06		
	PHS	11266	NPL	0.07			
Legault (1970)	DDR	19 experiments	NPT	0.11			
literature review	PHS	8 experiments		0.18			
Strang and King (1970)	DDR	3337	NPL	0.07	1 0.10		LW
		2371			2 0.06	1-2 0.10	
		1564			3 0.03	1-3 0.12	
		978			4 0.10	1-4 0.12	
		584			5 0.07	1-5 0.32	
Siler et al. (1971)	DDR	4151	NPT		1 0.18		LW
Cit. Johansson (1981)		–			2 0.15		
		1125			3 0.16		
Willeke and Richter (1978)	DDR	725	NPT		1 0.07		
		320			2 0.29		
	PHS	2535		0.06			
Strang and Smith (1979)	PHS	38000	NPL	0.04			LW
		35000		0.07			L
	DDR			0.07			LW
				0.09			L
Christensen (1980)	PHS	90000		0.13			
Cit. Johansson (1981)	DDR	11350		0.11			
Bolet and Felgines (1981)	DDR	6305	NPT		1 0.09		LW
		3915			2 0.08		
		2520			3 0.02		
		1484			4 0.11		
		6305	NPL		1 0.09		
		3915			2 0.08		
		2520			3 0.02		
		1484			4 0.09		
Johansson (1981)	PHS	6630	NPL	0.16	1 0.18		LW,L
		6630			2 0.15		
		4566			3 0.14		

DDR	daugher-dam regression	NPT	total number of piglets born
PHS	paternal half-sib analysis	LW	Large White
NPL	number of piglets born alive	L	Landrace

The estimates are based on daughter-dam regression or paternal half sib analysis.

ethods may differ between authors. Urban et al. (1966) regressed daughter's itter size on the size of the litter in which the daughter was born. Christensen 1980) regressed the mean of a daughter's litter performance on the mean of the am's litter performance. Heritability estimates are calculated for each parity, verall or for a sum of litters. The daughter-dam regressions are free from ominance effects but include maternal effects, which will bias the heritability stimates. Paternal half-sib estimates are free from maternal effects. There is, owever, no clear-cut difference between the estimates achieved using the two ypes of analysis. The heritability estimates for litter size at birth by both ethods are, on average, ~0.11. Analyses within parity number have revealed roughly he same heritability levels for parities 1, 2 and 3. Legault (1970) concluded that eritability for litter size at weaning is slightly lower while Johansson (1981) tated that the heritability for litter size at birth is at the same level as for itter size at three weeks. If the heritability for piglet mortality is zero one ight expect a somewhat lower heritability for litter size at weaning.

t is very difficult to get reliable estimates of heritability for litter size. here are no "test stations" for litter size which could produce data sets suitable or estimating genetic parameters.

arge data sets are necessary to obtain accurate estimates but those data are most ften collected in the field and several problems arise.

The number of animals within a herd-month subclass is often small. This makes it necessary to define periods of years or semesters instead of months. A small number of litters per subclass results in unreliable estimates of the subclass means, hence correction for the herd by period interaction introduces errors.

Especially in an "efficient" selection programme boars are used for a short period of time. This introduces the confounding of the boar and period effects.

Data sets may be not complete in the sense that farmers do not always record all data.

Culling of sows for low fertility will bias heritability estimates.

Herd management may influence the heritability of litter size as it affects the size of the environmental variance component. Hormonal induction of oestrus, a variable oestrus number at insemination of the gilt, housing, feeding etc. may be important factors. Variation in herd management could also affect the heritability.

Correction for factors as

- oestrus number at insemination before the first litter
- halothane susceptibility
- abortion

- hormonal induction of oestrus etc.

is frequently not possible as those variables are not recorded.
This may explain the large range in heritability estimates (0 to 0.30) and perhaps also the low average value. Johansson (1981) concluded from a literature review that the average heritability for litter weight tends to be slightly higher than for litter size. The mean piglet weight heritabilities are again somewhat higher (~0.3).

2.2.2 Influence of maternal effects upon heritability estimated by daughter-dam and granddaughter-granddam regression.

The maternal influence may result in a difference between heritability estimates by daughter-dam and granddaughter-granddam regression.
Revelle and Robison (1973), Alsing et al. (1980) and Vangen (1980) report granddaughter-granddam regression estimates of 0.2 to 0.3 while daughter-dam estimates averaged ~0.10 (table 2.2).

Table 2.2 Comparison between heritability estimates for litter size obtained by daughter-dam and granddaughter-granddam regression.

author	kind of daughter-dam pair	trait	heritability estimates by regression of: daughter on dam	granddaughter on granddam
Revelle and Robison (1973)	daughters' first litter on dams' first litter (birth litter?)	NPL	0.13±0.06	0.28±0.26
Alsing et al. (1980)*	daughters' first litter on dams' birth litter	NPL NPT	0.12±0.06 0.04±0.06	0.18±0.18 0.18±0.18
	daughters' first litter on dams' litter which is not the birth litter	NPL NPT	0.27±0.07 0.25±0.07	
Vangen (1980)	daughters' first litter on daughters' birht litter	NPL	0.08±0.08	0.29±0.18
	daughters' second litter on daughters' birth litter		0.44±0.11	
Willeke and Richter (1978)	daughters' first litter on dams' first litter	NPT	0.07±0.08	
	daughters' first litter on dams' second litter		0.25±0.08	
	daughters' second litter on dams' first litter		0.30±0.15	
	daughters' second litter on dams' second litter		0.29±0.12	

* *regression coefficients given by Alsing et al. (1980) were used to calculate heritability estimates by multi*plying the daughter-dam and granddaughter-granddam regression coefficients by 2 and 4 respectively. Taking the maternal effect into account they calculated a heritability for NPL and NPT of 0.30 and 0.29 respectively.

Taking the birth litter of a daughter into account also revealed some interesting phenomena. The regression coefficient of daughters' first litter on dams' birth litter was lower than the regression coefficient of daughters' first litter on dams' litter which was not the birth litter (Alsing et al., 1980). This is in agreement with the hypothesis that maternal influences upon gilts' litter size are important. Vangen (1980) found a higher regression coefficient for daughters' second litter on daughters' birth litter compared with the coefficient for daughters' first litter on daughters' birth litter (table 2.2). Also Willeke and Richter (1978) found similar results. This indicates that maternal influences upon daughters' second litter are smaller than the maternal influences upon the first litter.

It can be concluded that maternal effects bias the heritability estimated by daughter-dam regression but the heritability estimated by granddaughter-granddam is biased to a much smaller extent. The results indicate that litter size at birth has a heritability higher than 0.10 and they demonstrate the necessity of analysing litter size data in detail.

2.3 Selection experiments

2.3.1 Selection for litter size

Several selection experiments have been performed with the intention of increasing litter size, especially in mice. Results of five of these selection experiments are given in table 2.3 as partly summarized by Vangen (1981).

Table 2.3 Response to selection for litter size in mice.

	no. gen.	realized heritability		litter size (first litter) at the end of the experiment			standardization level
		H	L	H	L	C	
Falconer (1960)	30	0.08	0.22	9.3	5.9	7.6	N
Bradford (1968)	10	0.18		10.7		7.7	≤10
Joakimsen and Baker (1977)	14-15	0.18	0.22	14.0	6.5	9.4	≤8
Bakker et al. (1978)	29	0.11		13.8		8.1	N
Eisen (1978)	12	0.16		15.4		12.2	8

H = selection for high litter size; L = selection for low litter size; C = control line; N = no standardization.

These experiments show that it is possible to select for litter size successfully. Falconer did not standardize the litters but selection for litter size was done within litters. A relatively low realized heritability was obtained by Bakker et al. (1978).The reason for this might be that the absence of standardization results in a negative covariance between direct genetic and maternal effects which in turn, results in a lower realized heritability. This agrees with observations made in section 2.2.2.

Increased ovulation rate was found to be the reason for the increase in litter size. Bakker et al. (1978) also found lower pre- and post-implantation losses as a cause of the difference between the high and low line in the 16th generation. The difference between the high litter size line and the control in the Dutch experiment (continuation of the experiment reported by Bakker et al. (1978)) was also studied in the 50th generation. A new control line originating from the same base population as the previous one was introduced at the 46th generation of the high litter size line. There was no response to selection for litter size from generation 30 onwards. These two Dutch lines were compared with the 34th generation of the Norwegian high litter size line (continuation of the high litter size line reported by Joakimsen and Baker (1977)).

Results of this experiment (Van der Ploeg, 1982) and the Norwegian one (Joakimsen and Baker, 1977) are given in table 2.4.

Table 2.4 Means and number of observations of some factors determining litter size at birth.

trait	Van der Ploeg (1982)			Joakimsen and Baker (1977)	
	control line (D)*	high litter size line (D)*	high litter size line (N)*	high litter size line	control line
Number of first litters dissected at day 13 of gestation	106	109	94		
Average number of implantation sites**	11.7 (100)	17.8 (152)	17.3 (148)	17.1 (150)	11.4 (100)
Average number of foetuses alive at day 13	10.1 (100)	15.7 (155)	15.5 (153)		
at day 16				15.0 (144)	10.4 (100)
Average number of foetuses alive as a percentage of the number of implantation sites at day 13	86 (100)	88 (102)	90 (104)		
at day 16				88 (96)	91 (100)
Number of litters born	112	105	95		
Average number of young born (total)	9.9 (100)	14.4 (145)	13.4 (135)	14.0 (144)	9.7 (100)
Average number of young born as a percentage of the number of implantation sites	85 (100)	81 (96)	77 (92)	82 (96)	85 (100)
Average number of young born alive	9.8 (100)	13.9 (142)	13.2 (135)	13.7 (144)	9.5 (100)
Average number of young born alive as a percentage of the number of implantation sites	84 (100)	78 (93)	76 (91)	80 (96)	83 (100)

Figures in parentheses are selected lines as a percentage of the control line of that study.

* D = Dutch; N = Norwegian

** The number of implantation sites was calculated as the sum of the number of embryos alive, the number of dead embryos and the number of black, somewhat elevated, spots on the uterus wall.

The number of implantation sites had increased by 50% in the selection lines compared with the control lines. The percentage of young born (alive and dead) was somewhat lower in both selection lines than in the control lines. Selection response in both high litter size lines could be explained by a higher number of implantation sites and, very probably, by a higher ovulation rate.

In all experiments the selection criterion was litter size at first parity. Wallinga and Bakker (1978) studied the effect of long term selection for total number of mice in the first litter on lifetime performance of females from generation 25. Within the high litter size line the effect of standardization of litter size at birth to eight young was studied. Males were removed from the female just before littering and were returned when the litter was weaned. Total production of young in the high litter size line was much higher than in the control line because higher litter size was maintained at subsequent parities. Standardization of litter size did not significantly influence the total production of young.

Two selection experiments for litter size in pigs have been reported. Ollivier and Bolet (1981) reported a selection experiment for litter size in France. It was started in 1965 and the results of the first ten generations and some of the results of the eleventh generation have been published by Ollivier and Bolet (1981) and Bolet and Ollivier (1982) respectively. They selected on the sum of first and second litter size. Results are given in fig. 2.2. The positive response observed at first over five generations per litter was not confirmed in the following ones and the trend observed over the whole experiment was essentially zero. The positive trends for number of corpora lutea and number of embryos alive at 30 days of gestation after the second litter were not significant. A second experiment was started in 1976 in Madison, Wisconsin, U.S.A. Selection for increased litter size (defined as the number of fully formed piglets born) was practised among females in lines S and N. In line S, litters were reduced within 24 hours of birth to 6 piglets. In line N fraternity sizes were not altered. Results of 3 generations of selection were given by Rutledge (1980) and are illustrated in figure 2.3. These results suggested that standardization of litters removed at least part of the negative covariance between maternal and genetic effects and hence facilitated selection for litter size. More generations are needed to prove this theory.

2.3.2 Selection for ovulation rate

Two studies on mice (cited by Vangen (1981)) have been reported for ovulation rate. Bradford (1969) found realized heritability of 0.10 while Land and Falconer (1969) found it to be 0.33. No increased litter size was found in any of these studies. This was confirmed in the 9 generation selection experiment for high ovulation rate in pigs reported by Cunningham et al. (1979). Results of this experiment are given in figure 2.4.

Realized heritability was 0.42 while there was no significant response in litter size. Cunningham et al. (1979) conclude that the lack of correlated response in litter size is due to a reduction in fertilization rate and/or prenatal survival in the selected line.

The results of selection for ovulation rate and litter size in mice and pigs appear

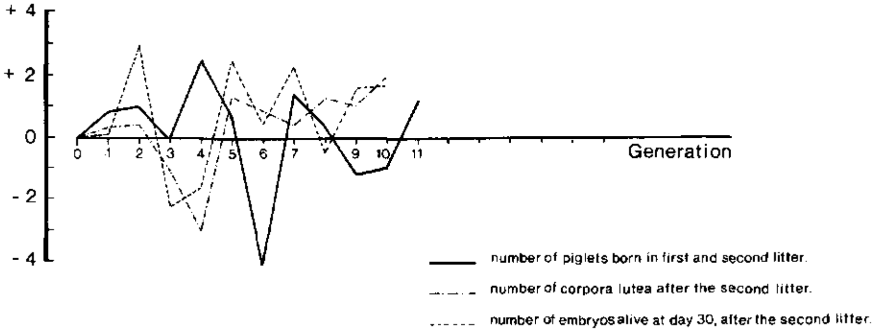


Fig. 2.2 Differences between the selection and the control line (Ollivier and Bolet, 1981; Bolet and Legault, (1982).

Fig. 2.3 Differences between the selection lines and the control line (Rutledge, 1979).

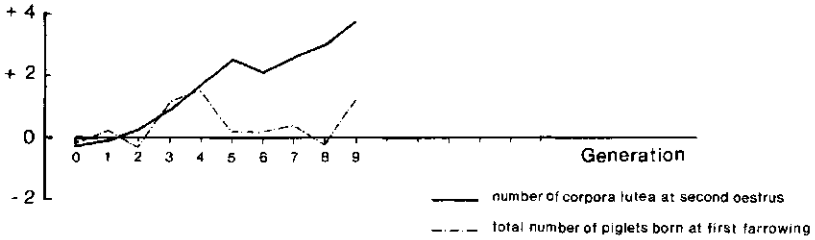


Fig. 2.4 Difference between the selection and the control line (Cunningham et al., 1979).

to suggest that the magnitude and sign of the genetic correlations between ovulation rate, pre-natal survival and litter size depend upon the particular trait being selected. Ovulation rate, fertilization rate and pre-natal survival are all components of litter size. Thus, selection for litter size would be a type of index selection (Cunningham et al., 1979). If ovulation rate and pre-natal survival are negatively related genetically, then selection for increased ovulation rate would result in a reduction in pre-natal survival. Effects on litter size might not be expected. However, selection for litter size (an index) might apply enough selection pressure on the component traits to overcome negative genetic relationships among the components. Litter size selection could increase ovulation rate and maintain pre-natal survival, resulting in increased litter size. This "natural index" is the easiest way of combining the component traits. Whether this index is optimal depends upon the phenotypic and genetic correlations between, and the heritabilities and variability of, the component traits. These parameters are not necessarily the same in mice and pigs.

2.4 Estimates of maternal effects

Several experiments have been carried out to estimate the size of the maternal effect upon litter size. Most experiments used the mouse as a model for pigs. In only a few experiments were pigs used.

Estimates of the post-natal maternal influence (m_2) or the total maternal influence ($m_1 + m_2$, assuming a phenotypic correlation of 1 between litter size at birth and litter size during the suckling period) as determined by litter size are given in table 2.5.

Table 2.5 Coefficients of post-natal (m_2) and total ($m_1 + m_2$) maternal effect.

author	m_2	m_1+m_2	species	trait
Falconer (1965)		-0.13	mice	
Nelson and Robison (1976a)	-0.05		mice	total number born
Eisen and Durrant (1980b)	-0.09		mice	number born alive
Van de Groes (1978)	-0.13		mice	total number born
De Boer (1983)	0.00		mice	total number born
Nelson and Robison (1976b)	-0.11		pigs	total number born
	-0.15			number born alive
Alsing et al. (1980)		-0.12	pigs	total number born
		-0.08		number born alive
Rutledge (1980)	-0.20		pigs	total number born

Falconer (1965) obtained a value for the coefficient of the maternal effect ($m_1 + m_2$) of -0.133 using data of a selection experiment with mice in which he selected for high and low litter size. Partial regression coefficients allowed a separation of the overall regression of daughters' on dams' litter size into two parts, one associated with the daughters' weight and the other independent of the daughters' weight. The former represented the coefficient of the maternal effect ($m_1 + m_2$) as estimated by means of daughters' weight. This was obtained by multiplying the regression of daughters' weight on mothers' litter size by the partial regression of daughters' litter size on daughters' weight (with mothers' litter size constant). A value of -0.098 was obtained. This is illustrated by figure 2.5.

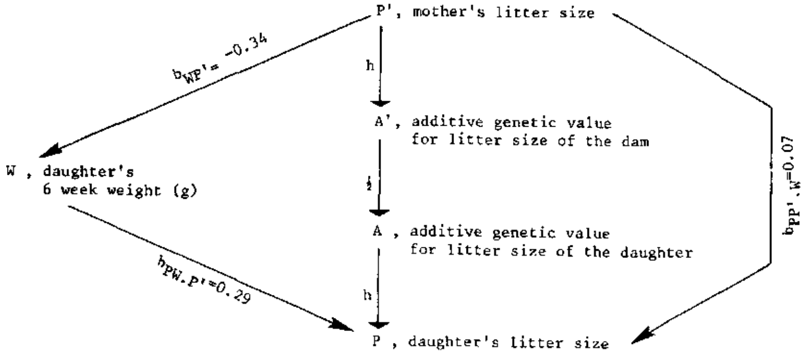


Fig. 2.5 Relationships between litter size and body weight at 6 weeks of age in mice

Falconer (1965) concluded that the major part of the maternal effect seemed to operate through the growth of the daughters as expressed in their adult weight at 6 weeks of age.

Nelson and Robison (1976b) studied the influence of post-natal litter size in pigs by standardizing litters after birth at 6 or 14 piglets per litter. Results are summarized in table 2.6.

Table 2.6 Influence of litter size in which gilts were raised upon production and reproduction traits (Nelson and Robison, 1976b).

	Standardization level				
	6	(n)	14	(n)	Difference
Birth wt (kg)	1.33	(178)	1.35	(171)	-0.02
14-day wt (kg)	4.06		3.57		0.49**
28-day wt (kg)	7.36		5.94		1.42**
42-day wt (kg)	10.96		8.19		2.77**
56-day wt (kg)	16.51		12.02		4.49**
140-day wt (kg)	70.9		65.5		5.4
Backfat thickness (mm)					
shoulder probe	28.7		29.2		-0.5
loin probe	21.8		22.3		-0.5
Age at first oestrus (d)	208	(94)	206	(89)	2
No. of corpora lutea	12.96	(56)	11.95	(57)	1.01*
No. of embryos at appr. 25 days of pregnancy	11.06		9.88		1.18+
Total no. of piglets born	9.19		8.31		0.88

+ = $p < 0.10$ * = $p < 0.05$ ** = $p < 0.01$

Piglets raised in small litters were heavier at weaning (56 days) and at an age of 140 days. Slightly lower backfat thickness (0.5 mm) at 72.7 kg was noted for females raised in small compared with large litters, but the difference was not significant. Fredeen and Plank (1963) found the reverse. Percentage of gilts which failed to show oestrus, age at first oestrus and conception rate seemed to be equal for both groups. Those data were not very reliable as observation for first oestrus was in one replicate only for a short time and omitted altogether in an other one (there were 4 replicates). The number of gilts which were inseminated was not given. The number of corpora lutea, the number of embryos and the total number of piglets born were higher for gilts raised in small litters. It was not clear whether the oestrus number at insemination was equal for both groups. Similar experiments were carried out with mice (Nelson and Robison, 1976a; Eisen and Durrant, 1980a; Van de Groes, 1978; De Boer, 1983).

Estimates of the post-natal maternal influence upon litter size as determined by the standardization level applied are given in table 2.5.

The average value for m_2 in mice is -0.07. Results of two experiments with pigs have been reported (Nelson and Robison, 1976b; Rutledge, 1980). The latter reports a value for m_2 of -0.26. However, the design of the experiment in which this value was obtained was not entirely satisfactory.

Three lines were involved in this experiment.

S selection for litter size; litters standardized at 6 piglets per litter.
N selection for litter size; litters not standardized.
C control line; litters not standardized.

Results are complicated as pre-natal, post-natal and selection effects are involved. Assume the following model

$$P = \mu + m_1 P'_b + m_2 P'_s + S$$

P = phenotypic value (line mean)
P'_b = litter size at birth of birth litter
P'_s = litter size during the suckling period of the birth litter
S = response to selection
m_1 = regression coefficient for pre-natal maternal influence
m_2 = regression coefficient for post-natal maternal influence.

Summarized results were

S $11.3 = \mu + 11.3\, m_1 + 5.8\, m_2 + S_s$
N $10.2 = \mu + 10.2\, m_1 + 10.2\, m_2 + S_n$
C $10.8 = \mu + 10.8\, m_1 + 9.1\, m_2$

The equations for the N and C lines are rather similar. For this reason the S equation was compared with the other two. Assuming values for m_1,S_s and S_n results in estimates of m_2. If $S_s = S_n = 0$ and m_1 is 0 or -0.10, resulting values for m_2 are -0.20 and -0.22 respectively. If $S_s = S_n = 0.2$ the values for m_2 are -0.17 and -0.19 respectively. So an estimate for m_2 of -0.20 seems reasonable. A value of -0.11 has been obtained by Nelson and Robison (1976b). Thus, there is considerable uncertainty about the parametric value.

Results given in table 2.5 suggest that pre-natal maternal effects are smaller than post-natal maternal effects as determined by the size of the litter. No estimates of m_1 are available. The maternal influence in mice upon weight of the young is summarized in table 2.7. Increase of standardization level from 8 to 16 reduced the weaning weight of individuals by approximately 35%.

Table 2.7 Influence of standardization level during the suckling period upon weight of the young in mice.

	Body weight (g)			
author	12 days pp	21 days pp	42 days pp	56 days pp
Eisen and Durrant (1980a)				
STL = 8	9.50 (100)	15.40 (100)	29.30 (100)	
12	7.96 (84)	13.63 (89)	28.31 (97)	
16	6.53 (69)	11.27 (73)	26.53 (91)	
Nelson and Robison (1976a)				
STL = 8	8.87 (100)	13.83 (100)	26.11 (100)	
14	6.54 (74)	10.63 (77)	23.59 (90)	
Van de Groes (1978)				
STL = 8	7.65 (100)	13.84 (100)		30.22 (100)
12	5.73 (75)	9.84 (72)		28.95 (96)
16	4.74 (62)	7.84 (57)		27.08 (90)
De Boer (1983)				
STL = 6		12.80 (111)		24.37 (102)
8		11.57 (100)		23.90 (100)
10		10.63 (92)		23.81 (100)
12		9.12 (79)		22.42 (94)
14		7.70 (67)		21.52 (90)

2.5 Influence of oestrus number at insemination on first litter size

Pay and Davies (1973), MacPherson et al. (1977)and Young and King (1981) studied the influence of oestrus number at insemination on reproductive performance of gilts. Those results are summarized in table 2.8.

Average conception rates (weighted for the number of gilts mated) for gilts bred at first or third oestrus were 75 and 86% respectively. The difference in total number of piglets born is approximately 1.8 piglets. Piglets born in litters of gilts bred at the third as compared with the first oestrus were slightly heavier.

Table 2.8 Reproductive performance of gilts bred on first, second or third oestrus.

	Pay and Davies (1973)			MacPherson et al. (1977)			Young and King (1981)	
oestrus number at insemination	1	3	3	1	2	3	1	3
Breed	LW * (L * LW)			L * LW			Yorkshire	
Feeding level (kg/d)	1.4	1.4	2.3	restricted			2.5	2.5
during the period:	55 kg to service			30 kg to service			120 days of age until 25 days post breeding	
Feeding level from service to parturition (kg/d)	1.4	1.4	1.4	2.2	2.2	2.2	-	-
No. of gilts mated	41	28	29	47	13	15	56	53
Conception rate (%)	72.5	91.3	89.6	83	100	93	69.6	77.4
Weight of gilts at service (kg)	77.1	96.5	115.8	90	98	115	91.7	-
No. of gilts farrowed	30	26	26	37	18	17	32	32
Total number of piglets born	-	-	-	7.8	9.8	10.4	9.6	10.6
No. of piglets born alive	7.90	9.27	9.88	7.7	9.6	9.8	9.3	10.0
Mean birth weight (kg)	1.15	1.23	1.23	1.29	1.24	1.16	1.07	1.15

LW = Large White; L = Landrace

Hughes and Cole (1975)stated that the average age at first oestrus reported is about 200 days. Young and King (1981) report recent experiments in which the average age at first oestrus was between 180 and 200 days.

In an experiment by Hughes and Cole (1975) neither gilt age nor weight at puberty significantly affected ovulation rate at second oestrus, conception rate or embryo survival during the first 20 days of gestation.

2.6 Influence of halothane susceptibility upon production and reproduction traits

The susceptibility of the meat pig to stress, and abnormal meat quality - in particular pale, soft, exudative (PSE) muscle - has been the subject of much research. The halothane-test was introduced as a non-lethal diagnostic method in the live pig by Eikelenboom and Minkema (1974). The differences in production traits which were found between the halothane phenotypes were summarized by Eikelenboom (1981) as follows:

- The growth rate was lower in reactors owing to their lower feed intake under ad lib conditions. No significant differences were found, however, under restricted feeding conditions which were also practised at the testing stations.
- Death losses due to stress were consistently higher in reacting pigs than in non-reacting pigs. Losses during the fattening period in (individually housed) boars and gilts as well as those recorded during the transport of the gilts to the slaughterhouse, were approximately ten times higher in reactors than in non-reactors.
- Meat quality was inferior in reactors as evidenced by their lower pH and higher muscle temperature and rigor values at 45 min. post mortem, lower quality score and higher transmission percentage observed at 24 hours post mortem.

- A lower backfat thickness and carcass length, and a higher dressing-, ham-, shoulder- and total meat percentage was found in reactors. This increased meat percentage was due not only to a decreased fat percentage, but also to an increased meat to bone ratio.

Some reported differences between halothane positive (HP) and halothane negative (HN) pigs from 20 studies were summarized by Webb et al. (1982) and given in table 2.9.

Table 2.9 Summary of some reported differences in performance between halothane positive (HP) and negative (HN) pigs from a variety of breeds and countries (Webb et al., 1982).

		Difference: HP - HN		
			Range	
	Number of studies	Mean	Minimum	Maximum
Growth traits (approx. 25-90 kg)				
Growth rate (g/d)	12	-2	-47	28
Daily food consumption (kg)	9	-0.07	-0.46	0.06
Food conversion ratio (food/liveweight gain)	11	-0.06	-0.30	0.02
Carcass traits (approx. 90 kg)				
Lean (% by weight)	8	2.6	0.9	4.6
Ham (% by weight)	7	0.7	0.3	1.0
Average backfat (mm)	14	-1.0	-4.0	1.0
Killing out %	6	1.0	0.2	2.6
Eye muscle area (cm²)	7	1.1	-2.7	3.4
Carcass length (mm)	9	-11	-29	1
PSS traits				
Postweaning mortality (and transport losses (%))	3	9.8	4.7	17.0
PSE (% of carcasses)	4	46	22	80
Meat colour (% paler than HN)*	14	15	0	50
Meat quality (% worse than HN)*	7	31	16	78
pH 45 min post mortem	11	-0.31	-0.66	0.02
CK activity (log units/litre)	6	0.50	0.06	0.79
Reproduction				
Conception rate (%)	1	-24	-	-
Litter size born alive	1	-1.6	-	-
Litter size at weaning	1	-1.1	-	-
Estimated economic return per pig marketed for bacon at 90 kg in UK (£)	-	-3.92	-10.57	3.54

* Differences expressed as 100 x (HP - HN)/HN

Equal weighting was given to each study, in calculating the mean, irrespective of breed, feeding regime or statistical significance.

In Dutch testing station studies (Eikelenboom et al., 1978, 1980) it was found that the selection index of reacting boars was significantly superior to that of non-reacting boars (110 vs. 100 and 108 vs. 98 respectively, in both studies). The boar index, which has an average of 100 and a standard deviation of 33 points, is based upon the boar's growth rate, feed conversion and ultrasonically measured backfat thickness, in addition to growth, carcass and meat quality traits of the full sibs. The inferior meat quality of reactors is more than outweighed in the

index by their higher meat percentage and thinner backfat compared with non-reacting animals. Hence, if there were no selection against halothane susceptibility, the percentage of reactors would probably increase.
Conception rate and litter size in halothane positive pigs were reduced by contrast with halothane negative pigs, but this finding was from one experiment only (Webb, 1980, 1981).

2.7 Year-season effects

Differences between years and seasons, for production as well as reproduction traits, have frequently been reported in the literature. A review has been made by Ketelaars (1979). No further attention will be paid to those influences as they were not the main objective of this study but merely disturbing influences which had to be considered.

3 MATERIALS AND METHODS

3.1 Experimental design

The maternal influence upon litter size seems questionable because no systematic differences in h^2, estimated by daughter-dam regression or paternal half sib analysis, have been found (Johansson, 1981). The maternal influence affects h^2 estimated by daughter-dam regression while it does not affect h^2 estimated by paternal half sib analysis. On the other hand Nelson and Robison (1976 b) found a negative influence of being raised in large litters upon weight of the gilt and the size of its first litter. Experiments with mice gave similar results (Nelson and Robison (1976 a), Eisen and Durrant (1980). Indirect indications of the maternal influence upon litter size in pigs were found by Alsing et al. (1980) and Rutledge (1980).

Maternal influences are partly due to the litter size during the suckling period. Two hypotheses have been postulated. Firstly litter size during the suckling period could influence weaning weight, development of the pig, age at first oestrus and subsequent first litter size (Nelson and Robison, 1976 a; Robison, 1979). Secondly it could also affect the size of the pool of primordial follicles present at weaning of the piglets (Rutledge, 1980). An experiment was designed to test the first hypothesis.

The experiment was designed to estimate the effect of standardization level (litter size during the suckling period) upon the development of the gilt, age at puberty, size of the first litter and number of corpora lutea after first oestrus of the weaned primiparous sow. The estimates had to be

- free from grand maternal effects
- not confounded with additive genetic effects.

For these purposes four batches of Dutch Landrace gilts were put in the experimental unit at an age of approximately 74 days. They were born and raised to a weight of ca. 25 kg at 15 farms in the south of The Netherlands. The size of the farms and type of housing was average by Dutch standards but their management was generally above average. They could be marked as multiplier herds which produced their own replacement gilts. Gilts of the fourth batch had to be kept at one farm from 25 to approximately 50 kg because of swine fever before they were transported to the experimental unit in Wageningen. Four batches of 48 gilts were bought at three monthly intervals. Gilts of the first batch were born in May 1976. The experimental capacity came to 144 places for rearing gilts and 24 farrowing pens. Every three months 24 litters could be produced and out of those litters 48 gilts were selected to be reared. The four batches of gilts which were purchased consisted of 24 pairs of litter mates to obtain a similar "litter structure" for batches which were bought and produced thereafter.

The experiment was carried out at the experimental unit "De Haar" of the Agricultural University in Wageningen. The experimental design is given in figure 3.1.

eneration		
1	192 bought-in gilts (batches 1 to 4)	
	↓	
2	ca. 96 litters produced and standardized at 8 piglets/litter (batches 5 to 8)	
	↓	
2	192 gilts selected (batches 5 to 8)	
	↓	
3	ca. 96 litters produced (batches 9 to 12)	
	ca. 48 litters, standardized at 12 piglets per litter (H)	ca. 48 litters, standardized at 6 piglets per litter (L)
	↓	↓
3	96 gilts	96 gilts selected (batches 9 to 12)
	↓	↓
4	ca. 48 litters	ca. 48 litters produced (batches 13 to 16)

ig. 3.1 The experimental design.

Generation-2 gilts were raised in litters which were standardized at 8 piglets per litter after birth (see 3.4). Only gilts which were raised by their own dam in litters of 6 or more piglets at weaning were selected to produce the third generation litters. This minimum of 6 piglets was necessary to make sure that all generation-2 gilts were exposed to the same post-natal maternal influence as determined by litter size during the suckling period. This results in equal post-natal grand maternal effects as determined by litter size during the suckling period for generation-3 gilts. Crossfostered gilts were not selected as cross-fostering might have influenced the performance of gilts.

Generation-3 litters were standardized at 12 (high level) or 6 (low level) piglets per litter. Gilts raised by their own dam in litters of ≥9 or ≥4 respectively at weaning were selected to be reared and to produce the fourth generation litters. This minimum of 9 (high standardization level) or 4 (low level) piglets was necessary to make sure that generation-3 gilts were exposed to either a high or low size of the litter in which they were raised. The weaning weights of the one upto three selected female piglets per litter had to be as close to the litter average as possible. This resulted in a decrease of the within litter variance of selected gilts and also in a relatively small variance within pens during the rearing period (four gilts per pen) which was considered to be desirable as gilts

were not individually fed.
Routine herd management procedures were followed, including the administration of Fe injections to the piglets at 2 days of age and antibiotic treatment for piglets and gilts as necessary. Boars were castrated at an age of two to three weeks. Piglets were weaned at five weeks of age.
Oestrus detection once a day started at an average age of 168 days. Oestrus detection was initially by a visual inspection followed by checking the acceptance reflex using vasectomized boars.
Gilts were artificially inseminated once during a fixed three week insemination period for each batch. This insemination period started at an average age of the batch of 245 days. Dutch Landrace boars were chosen at random and a boar was used only once during an insemination period. The use of one boar for all gilts would ha decreased the genetic variation but for practical reasons was not possible. The use of a limited number of boars could have caused a confounding of the standardizatio level effect with the boar effect. Gilts produced their first litters at an age of approximately one year, so a pattern of four batches per year and per generation was maintained. The last batch of litters of generation four was born in February 1980 (16th batch).

3.2 Housing

Type of housing is given in table 3.1. Water from nipple drinkers was always available.

Table 3.1 Housing.

Age of the gilts (on average)	name	group size housing	feeding	floor type	bedding
0-35 days	nursery	litter	litter	concrete	straw
35-74 days	rearing	litter	litter	partially slatted	woodshavings
74-230 days	rearing	4	4	partially slatted	woodshavings
230 days-4 weeks before parturition	rearing	4	1	partially slatted	straw
4 weeks before parturition-weaning	nursery	1	1	concrete	straw

As far as possible two pairs of litter mates (four gilts) were put together in one pen at an average age of 74 days. Generation-3 gilts out of one standardization level were put together in order to assure that high and low standardization level gilts were fed similarly.
The age range within a batch could be 20 days or less. The change of housing always occurred at the same day for the whole batch (except weaning) resulting in a somewhat variable age when this took place.
Temperature was kept at approximately 17°C by a central heating system. During

summer it was not always possible to keep the temperature below 17°C. Gas heaters were used in the nursery to increase the temperature for the new born piglets.

3.3 Feeding

The feeding system varied with age. A summary is given in table 3.2. Gilts were fed twice a day from an average age of 74 days onwards.

able 3.2 Feeding system.

ge of gilts on average)	group size	amount	type of feed	amount weighed
0-21 days	litter	ad lib	pig starter	NO
1-35 days	litter	ad lib	creep	YES
5-74 days	litter	ad lib	creep	YES
4-230 days	4	scheme 1	creep/sow feed	YES
30 days-parturition	1	± 2.5 kg/d	sow feed	NO*
arturition-weaning	1	scheme 2	sow feed	YES

Gilts were hand fed. The total amount fed per batch was recorded to make sure that gilts received on average 2.5 kg per day

Scheme 1

The aim was to give 1.33 MJ ME/$W^{\frac{3}{4}}$ up to a weight of 40 kg and 1.26 MJ ME/$W^{\frac{3}{4}}$ from 40 kg onwards with a maximum of 2.5 kg sow feed (30.5 MJ ME, calculated). This scheme was comparable to that for breeding gilts recommended to farmers in The Netherlands (CBV, 1975), although the latter was calculated on body weight not on metabolic weight. Gilts were weighed every four weeks and the average weight of the four gilts in a pen determined the amount given to the gilts in that pen for the next weeks assuming a daily growth of 550 grams. Generation-3 gilts were weighed every two weeks. When the average weight of the four gilts in a pen reached 40 kg they were given a mixture of equal parts creep and sow feed for one week before going on to sow feed alone.

Scheme 2.

On the day of parturition the sows were not fed. Thereafter the sows gradually received more feed up to a maximum of 2.5 kg + 0.25 kg/piglet. Standardization levels of 6, 8 and 12 piglets resulted in the schemes given in table 3.3.

able 3.3 Feeding schemes during the suckling period.

g of sow feed	Standardization level 6	 8	 12
ay 1, 2	1.50	1.50	1.50
ay 3, 4	2.00	2.00	2.00
ay 5, 6, 7	2.50	2.50	2.50
ay 8-12	2.75	3.00	3.00
ay 13-16	3.25	3.50	4.00
ay 17-21	3.75	4.00	5.00
ay 22-35	4.00	4.50	5.50

The schemes were adjusted if a piglet died. Commercial feeds were used. The formulation of the sow feed is given in appendix 1.

3.4 Standardization

Parturition was induced to ensure synchronization and make standardization possibl
The following rules were applied:

- Piglets having a birth weight of 1 kg or less were as far as possible left out of the standardized litters to reduce piglet mortality.
- At least two gilts in each standardized litter had to be raised by their own mother in order to be able to select two gilts per mother after weaning.
- Litters were standardized at 6, 8 or 12 within 24 hours after birth.

3.5 Variables measured and calculated

The variables which were measured are given in appendix 7. Further details and variables which were calculated are described in this section. Explanation of symbols and abbreviations is given in appendix 8.

Weights and growth from birth to 56 days of age

Individual weights were used to calculate growth per day from day 0 to 21, 21 to 35, 0 to 35 and 35 to 56 (G0-21d, G21-35d, G0-35d, G35-56d). Average birth weight per litter was calculated making use of data from all piglets born live or dead (AW0b) and of piglets surviving up to 56 days of age (AW0s). Litter means for other weights and growth up to 56 days of age were also calculated using the data from surviving piglets.

Suckling frequency

Around day 9 and 29 after parturition the suckling frequency was recorded over a 2
hour period from feeding (8.00 h.) to feeding.

Milk consumption

Milk consumption of litters of generation 3 was measured by weighing the piglets just before and after suckling. At day 10 piglets were weighed individually while they were weighed in groups of six at day 30. The procedure was started at 8.00 h. by observing sow and litter, and separating the litter from the mother after the first suckling. Sixty minutes thereafter the piglets were weighed and put together with their mother. After the suckling, piglets were weighed and separated again from their mother. This was repeated four times,thus giving four readings for milk consumption. Den Hartog et al.(1983) concluded that a period of six hours seems to be sufficient for estimation of milk production. If the piglets failed to suckle the standard procedure was continued giving a suckling interval of 120 minutes. Weighing of the piglets was done with an electronic scale to the method described by Klaver et al.(1981).

The fourth measurement of milk consumption was not recorded after exactly 240 minutes. Corrected milk consumption per 240 minute period was calculated as the sum of the four successive milk consumption figures per litter multiplied by 240 and divided by the number of minutes between the suckling preceding the milk consumption measurement and the fourth suckling. This was done for data of day 10 and 30 giving MLT10 and MLT30. Milk consumption per piglet per 240 minute period was calculated as MLT divided by the number of piglets present at the milk consumption measurement giving MPT10 and MPT30.

In some cases a litter failed to suckle. This zero milk consumption was only partially compensated by an increased milk consumption afterwards and correction was necessary (see "results section 4.3.2").

Teat order at the udder

The teat order at the udder of generation-2 piglets (generation-1 mothers) was recorded at three successive sucklings at 21 ± 3 days after birth. The first pair of teats (left and right) was indicated as teat order 1. A piglet suckling 2 or 3 times a teat of the same order was given that order as the score. A piglet suckling teats of a different order at the three occasions was given the average score. A numerical example has been worked out in appendix 2. The teat order at the udder of generation-3 piglets (standardization level 6 or 12) was recorded at the days of milk consumption measurement (day 10 and 30).

Litter score for stability of teat order (TOSA, TOSB)

In order to analyse the teat order data it was necessary to develop a score to determine to what extent a teat order was established. A score was developed to determine how similar the three observed teat orders were.

Each piglet received a score using the following arbitrary criteria:

1. A piglet suckling the same teat three times: 10 points
2. A piglet suckling the same teat twice: 9-X points
   X is a deduction depending upon the teat the piglet suckled the third time and the nursing position of the sow.
   a) If the piglet changed suckling side because the sow changed side, X is the

number of places the pig was away from the teat it suckled twice -1.

   b) In all other cases X is the number of places the pig was away from the teat it suckled twice.

3. A piglet suckling a different teat three times: 6 points $-X_1$ $-X_2$. The main teat is the one which is closest to the other two teats suckled by that pig. X_1 and X_2 are the number of places the pig was away from the main teat at the two other sucklings.
4. A piglet sometimes not suckling.
   a) Not trying to suckle: normal score -2
   b) Trying to suckle but failing to obtain a teat: normal score -4.

The final litter score (TOSA) is the sum of scores for the individual piglets, divided by the number of piglets. An example has been worked out in appendix 2. TOSA combines several features of stability of the teat order which is desirable but also results in a parameter that indicates the degree of stability but does not specify which of the several factors give this result. A second score was developed. The number of piglets which suckled the same teat 3 times, 2 times or once (n_3, n_2, n_1) was recorded. The second litter score for stability of the teat order (TOSB) was calculated as $((2 * n_3) + n_2) / (n_1 + n_2 + n_3))$. The maximum values for TOSA and TOSB are 10 and 2 respectively.

Creep feed intake

Creep feed intake was measured from day 21 to 35 and 35-56 days after birth. Creep feed intake per piglet from day 21 to 35 (CFP21-35) was calculated as creep feed intake per litter divided by the average number of piglets alive. The average number of piglets alive was calculated as:

$$\sum_{i=22}^{35} NP_i \; / \; 14$$

where NP_i = number of piglets alive at day i. Creep feed intake per piglet from 35 to 56 (CFP35-56) was calculated in a similar way.

Halothane susceptibility

Piglets were tested for halothane susceptibility from batch 6 onwards at the age of approximately 60 days by a method described by Eikelenboom and Minkema (1974).

Weight at 74 days of age on average (W74)

During the rearing period all gilts within a group were weighed at the same day resulting in an age range of 20 days. An average of 74 days implies that the pigs were between 64 and 84 days old.

Backfat thickness

Backfat was measured ultrasonically at a fixed average age of 186 days and at a fixed weight of approximately 100 kg. In some cases, the two measurements coincided. The method is described by Bergström and Kroeske (1969).
Backfat thickness and heart girth of generation-3 gilts were also measured at parturition and weaning.

Growth and weight

The age at 25, 70 or 100 kg body weight was calculated by linear interpolation, e.g.

Wb = weight at last weighing before a gilt reached 25 kg body weight
Wa = weight at first weighing after a gilt reached 25 kg body weight
Ab and Aa: age at respectively Wb and Wa.

$$A25k = \text{Age at 25 kg} = Ab + ((Wb - Wa)/(Ab - Aa)) * (25 - Wb)$$

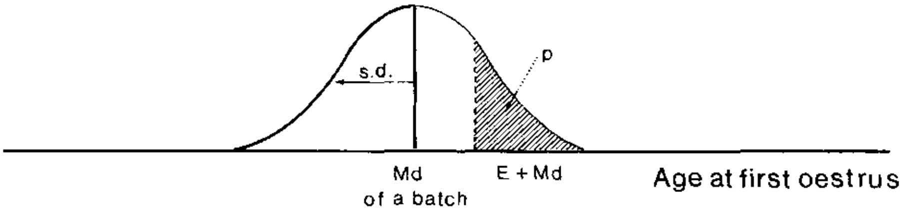
Weight at first oestrus and at insemination were calculated by linear interpolation between weights at weighings before and after a gilt reached first oestrus and between W216 and WEI.
Growth from 25 to 100 kg was calculated as 75000/(A100k-A25k).

Age at first oestrus

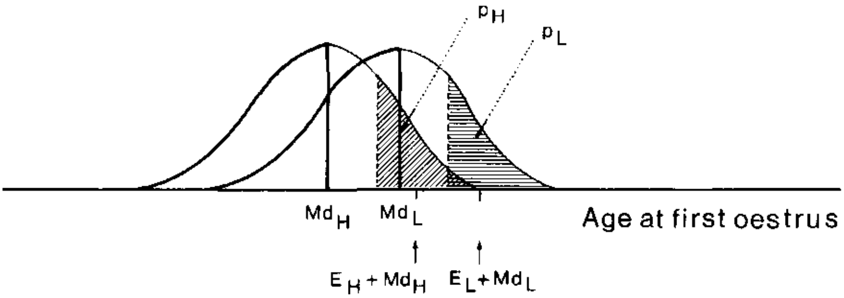
Two variables were calculated apart from age at first oestrus (AFO):

- age at first oestrus as a deviation of the batch median (AFOM)
- age at first oestrus as a deviation of the median supplemented by values for gilts which did not show first oestrus before the end of the insemination period (AFOMS).

AFOM was calculated to create a variable which expresses a value for a gilt in relation to the mean of the batch. The mean age at first oestrus was not known as a fraction of the gilts did not show first oestrus before the end of the insemination period. The median of a batch was used instead. AFOMS was calculated to combine age at first oestrus and the percentage of gilts which did not show first oestrus. The value for gilts which did not show first oestrus was estimated. The average standard deviation of the distribution left of the batch median was calculated and appeared to be 17 days. Combining this value with the fraction of gilts which did not show first oestrus (p), and assuming a normal distribution gives the estimated value (E).



The procedure for batches 9 to 12 was different. The batch median and the fraction of gilts which did not show first oestrus were calculated per standardization level.



The supplemented value for gilts at the high standardization level of a given batch was:

$$(E_H + Md_H) - ((Md_H + Md_L)/ 2) = E_H + \tfrac{1}{2} (Md_H - Md_L)$$

Values for gilts at the low level were determined in a similar way:

$$(E_L + Md_L) - ((Md_H + Md_L)/2) = E_H + \tfrac{1}{2} (Md_L - Md_H)$$

Number of piglets born

Farrowing gilts were checked regularly during daytime (8.00 - 17.00 h.) and at least once in the remaining period (at 23.00 h.). The total number of piglets delivered (NPT) was recorded and included those that were dead at recording plus any mummified piglets. This characteristic (NPT) was used in the analyses because it reflected the capacity of the gilt to produce piglets and because the number dead on recording consisted of both stillborn piglets and those dying soon after birth.

Oestrus after weaning

First oestrus after weaning of primiparous generation-3 sows was recorded. If sows did not show oestrus within 21 days of weaning, oestrus was induced with 400 I.U. of Pregnant Mare Serum and 200 I.U. of Human Chorion Gonadotrophin (PG 600® (Intervet B.V., Boxmeer, Netherlands)) intramuscularly. All animals were slaughtered within 7 days after oestrus or oestrus induction.
Weight of uterus (WU) and ovaries (WOV), number of corpora lutea (NCL) and length of right + left uterus horns (LUH) were recorded.

3.6 Statistical analysis

The SPSS-package (Nie et al, 1975) was used to perform tests of normality, to calculate correlation coefficients and to make frequency distributions and contingency tables. A least squares programme (Harvey, 1977) was used to perform analyses of variance and to estimate the effects of factors and covariables. The models were reparameterized by the least squares programme by making use of the sum restrictions. This programme applies the classic regression approach i.e. effects are estimated by adjusting for all other effects.
Data of 12 batches of gilts were available. Environmental variation between batches may be important. The batch effect was included in the models to correct the estimate of the standardization level effect for these environmental differences. This was done by distinguishing a generation-, a period- and a generation * period interaction effect. This was done as the first four batches were purchased and litters were standardized at 8 piglets, while gilts of batches 5 to 8 produced litters which were standardized at 6 or 12. Gilts of batches 9 to 12 were raised in litters of 6 or 12 and produced litters which were standardized at 8 or 9 piglets. Data of gilts of batch 4 were left out of the analyses because those gilts were transported to the experimental unit at a weight of approximately 50 instead of 25 kg and because of fertility problems (see table 4.1). Data of the 11 remaining batches were analysed according to the following basic model:

$$y_{ijkn} = \mu + Ge_i + Per_j + (Ge * Per)_{ij} + STL_{k:i=3} + e_{ijkn} \qquad \text{(model I)}$$

y = dependent variable
μ = overall mean
Ge_i = effect of generations. $i = 1, 3$
Per_j = effect of period of birth. $j = 1, 4$
$(Ge * Per)_{ij}$ = effect of generation by period interaction
$STL_{k:i=3}$ = effect of standardization level. $k = 1, 2$
This effect was nested within generation 3.

Covariables were sometimes added to this model to estimate the regression within subcells between the dependent variable and the covariables and/or to correct for these covariables.

Traits as litter size may be influenced by the oestrus number at insemination (ONI). For those dependent variables ONI was added to the model.

ONI_l = effect of oestrus number at insemination

$l = 1,3$ 1: $ONI = 1$ or $l = 1,2$ 1: $ONI = 1$
2: $ONI = 2$ 2: $ONI \geq 2$
3: $ONI \geq 3$

From batch 6 onwards halothane susceptibility was tested. Data of gilts of batches 6 up to 12 were also analysed according to the following basic model to correct the estimate of the standardization level for the halothane effect.

$$y_{ijkmn} = \mu + Ge_i + Per_j + (Ge * Per)_{ij} + STL_{k:i=2} + HAL_m + e_{ijkmn} \qquad \text{(model II)}$$

$i = 1,2$ (generations 2 and 3)
H_m = effect of halothane susceptibility. $m = 1,2$

Age at first oestrus was expressed as a deviation of the median and analysed according to models Ia and IIa which are equal to model I and II respectively ignoring the period and generation * period effects. Data of generation-3 gilts only were analysed according to model IIb which is comparable to model II after omitting Ge_i and $(Ge * Per)_{ij}$. These analyses have the advantage that only data of gilts raised in litters of 6 or 12 are involved but they have the disadvantage that the correction for the halothane and oestrus number at insemination effects are less accurate as fewer data are used to estimate these effects.

Piglets of one litter were housed together up to 56 days of age. Variables measured on individual piglets up to 56 days were analysed according to the model

$$y_{jon} = \mu + Per_j + L_{o:j} + e_{jon} \qquad \text{(model III)}$$

for generations 2, 3 and 4 separately and according to

$$y_{jkon} = \mu + Per_j + STL_k + (Per * STL)_{jk} + L_{o:jk} + e_{jkon} \qquad \text{(model IIIa)}$$

for generation-3 piglets.

$L_{o:jk}$= effect of litter nested within groups (random effect)

$(Per * STL)_{jk}$ = effect of period by standardization level interaction

These analyses were carried out to estimate the variance between litters in relation to the standardization levels applied. Litter means were calculated and analysed according to model I. Weight and growth data from birth to 56 days of age of gilts which were selected to be reared were analysed according to model I but in this case only data of gilts of generation 2 and 3 were available. Effects were tested against the error term in all models except III and IIIa in which the Per, STL and (Per * STL) effects were tested against the mean squares of the L effect.

4 RESULTS

4.1 Numbers, means and tests for normality

Table 4.1 shows for the three generations

- the number of gilts at the beginning of the rearing period (at an average age of 74 days)
- the number of gilts reaching a weight of 100 kg
- the number of gilts inseminated
- the number of gilts pregnant
- the number of litters produced.

Table 4.1 Number of gilts at different stages of the experiment.

batch no.	at start of the rearing period	at 100 kg	inseminated	pregnant	litters produced
1	48	46	39	26	23
2	48	39	31	24	23
3	48	45	34	22	21
4	(48)	43	20	15	11
1-4	192	173	124	87	78
5	48	45	35	25	25
6	48	44	35	26	25
7	48	47	35	22	22
8	31	31	23	13	13
5-8	175	167	128	86	85
9	48	44	42	25	25
10	48	47	38	27	25
11	48	47	37	29	29
12	48	47	44	34	32
9-12	192	185	161	115	111
1-12	559	525	413	288	274

The following reasons for not producing a litter were observed

1. death
2. leg weakness
3. not pregnant after insemination
4. not inseminated although the gilt showed first oestrus
   Some gilts did not show oestrus during the 3-week insemination period. Insemination on a Sunday was not possible. So gilts which came on heat on a Sunday but were not on heat on the Monday could not be inseminated.
5. not inseminated, no first oestrus before the end of the insemination period

6. abortion
7. other reasons.

Table 4.2 Number of gilts not producing a litter for the reasons noted above.

Reason	Generation 1	2	3	total	% of total	% of 285
Death	8	6	2	16	2.9	5.6
Leg weakness	17	11	9	37	6.6	13.0
not pregnant after ins.	34	36	44	114	20.4	40.0
not ins., first oestrus	8	5	3	16	2.9	5.6
not ins., no first oestrus	38	25	10	73	13.1	25.6
Abortion	2	0	1	3	0.5	1.0
Other reasons	7	7	12	26	4.7	9.1
1-7	114	90	81	285	51.0	100.0
% of total number of gilts	59.4	51.4	42.2	51.0		
total number of gilts	192	175	192	559		

"Fertility problems" (code 3, 4, 5 and 6) accounted for 72 % of the culled gilts. In particular "not pregnant after insemination" was an important reason for not producing a litter bearing in mind that gilts were only inseminated once.

Population means, high and low standardization level means and standard deviations are given in table 4.3. Normality (skewness and kurtosis) was tested for after correction of the data for the batch effect. On the basis of these results all variables were considered to be normally distributed in spite of the peakedness of the distribution of litter creep feed intake from 21 to 35 and 35 to 56 days of age. Homogeneity of variances within batches and standardization levels was tested (Bartlett and Cochran; SPSS-manova). Homogeneity of variances was not valid for age at first oestrus because of differences in variance between batches. Variances were not homogeneous for creep feed intake and milk consumption data because of a difference in variance between the high and low standardization level and for number of corpora lutea in primiparous sows because of a difference in variance between the sows with spontaneous or induced oestrus.

Batch means are given in figures 4.1 to 4.7. Weight at an age of 56 days varied considerably from batch to batch while this was not the case for weight at weaning (W35). Growth from 35 to 56 days was low for the 13th batch (figure 4.1). Variation of batch means for growth per day from 25 to 70 kg and 70 kg to insemination (fig. 4.3) was large. The correlation between batch means for these variables was low (r = -0.12).

At the beginning of the experiment (generation 1) weights around parturition (WBP and WAP) were lower compared with those at the end of the experiment (generation 3). This tendency was not yet present at an average age of 186 days (W186). Age at parturition was not equal for all batches.

Table 4.3 Population means, high and low standardization level means, number of gilts involved (n) and standard deviations of variables measured and calculated.

Variable		population			high standardization level			low standardization level	
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
	Data of individual gilts which were raised								
Weight (kg)									
W0	366	1.34	0.23	100	1.40	0.20	91	1.37	0.22
W21	366	5.76	0.93	100	5.18	0.79	91	6.27	0.88
W35	366	9.50	1.51	100	8.76	1.53	91	10.54	1.34
W56	366	17.95	2.83	100	16.62	2.90	91	18.60	2.70
W74	511	24.8	4.9	100	22.9	4.6	91	26.0	5.6
W130	557	57.2	7.4	100	56.0	7.4	91	58.4	7.8
W186	547	91.2	9.8	100	89.7	10.2	89	91.4	9.9
WFO	431	116.0	11.8	83	118.0	11.6	78	119.5	9.2
WIN	411	124.7	10.0	82	126.4	10.8	78	127.3	10.4
WEI	504	127.5	10.5	91	130.2	10.1	83	131.0	9.9
WBP	263	191.2	13.5	56	196.8	13.5	53	200.9	11.7
WAP	271	173.9	12.1	55	179.7	12.5	54	182.2	10.3
WW*	239	140.3	11.6	32	137.0	12.2	34	144.0	11.9
Growth (g/d)									
G0-21d	366	210	41	100	179	34	91	233	38
G21-35d	366	267	63	100	255	69	91	304	62
G0-35d	366	233	41	100	210	42	91	262	36
G35-56d	366	402	91	100	374	90	91	383	96
G25-100k	481	597	70	95	606	66	89	590	64
G25-70k	504	599	72	100	606	71	91	593	65
G70k-IN	503	506	60	91	526	48	83	521	51
Weight difference (kg)									
WBP-WIN	263	66.7	8.3	56	70.5	8.1	53	73.7	7.1
WBP-WAP	260	17.3	5.6	54	17.9	6.0	53	18.5	5.4
WAP-WW*	237	34.0	8.6	32	35.0	9.6	34	27.0	5.8
Backfat thickness (mm)									
BFA	545	11.82	2.33	100	11.53	2.09	89	11.35	2.11
BFW	526	12.34	2.02	98	11.95	1.88	89	11.55	1.93
Fertility									
AFO (d)	431	236	20	83	238	16	78	240	16
NPT	274	9.87	2.59	56	10.05	2.70	55	10.20	2.88
	Litter traits								
Weight (kg)									
AW0b	240	1.33	0.17	32	1.33	0.14	34	1.37	0.16
AW0s	240	1.36	0.15	32	1.38	0.12	34	1.40	0.15
AW21	240	5.84	0.74	32	5.00	0.52	34	6.39	0.55
AW35	240	9.46	1.19	32	8.41	1.00	34	10.68	0.94
AW56	240	17.10	2.30	32	15.81	2.13	34	18.76	2.22
Growth (g/d)									
AG0-21d	240	212	33	32	172	24	34	237	24
AG0-35d	240	231	33	32	200	28	34	264	26
AG21-35d	240	258	48	32	242	44	34	305	51
AG35-56d	240	362	81	32	351	72	34	384	87
Creep feed intake (kg)									
CFL21-35	238	8.44	5.19	32	14.07	6.83	34	6.52	3.85
CFL35-56	206	101.7	23.2	16	137.7	37.0	16	90.4	22.4
CFP21-35	66	1.18	0.64	32	1.28	0.62	34	1.12	0.66
CFP35-56	32	14.01	4.21	16	12.38	3.33	16	15.56	3.86
TOSA	138	9.32	0.85	32	8.55	1.09	34	9.38	0.75
Milk consumption (g)									
MLT10	66	853	229	32	1004	222	34	711	120
MLT30	66	791	211	32	914	188	34	676	162
MPT10	66	106	25	32	89.4	19.4	34	122.1	18.0
MPT30	66	100	29	32	82.4	18.4	34	116.8	27.1
AMLT	66	822	196	32	958	171	34	693	113
AMPT	66	103	24	32	85.9	158	34	119.4	174

* High and low standardization level means for sows which nursed a large or small litter.

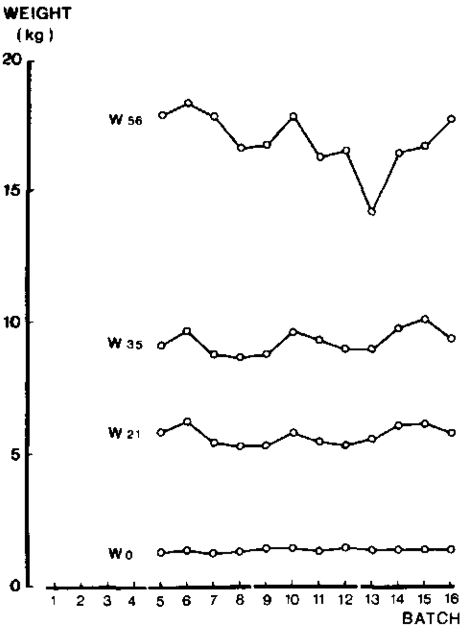


Fig. 4.1 Average piglet weights for each batch from birth up to 56 days of age.

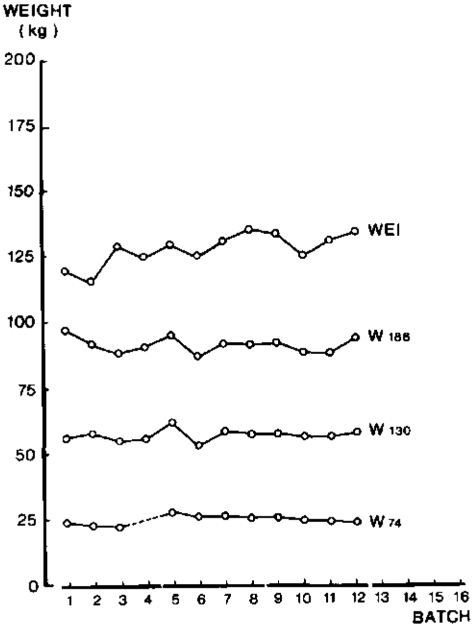


Fig. 4.2 Average body weight for each batch at an average age of 74, 130 and 186 days and at the end of the insemination period.

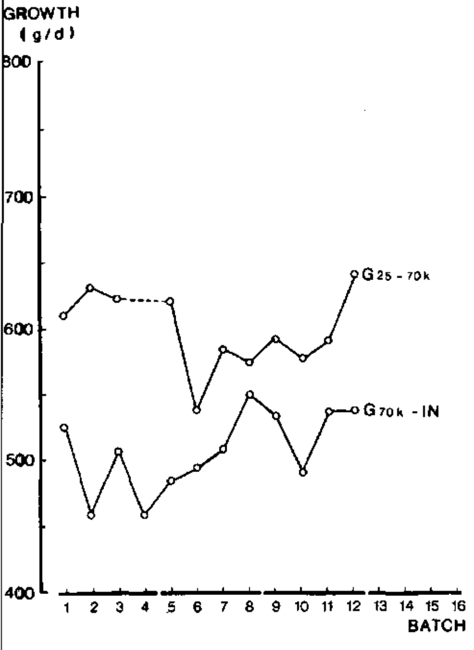


Fig. 4.3 Average growth for each batch from 25 to 70 kg and from 70 kg to the end of the insemination period.

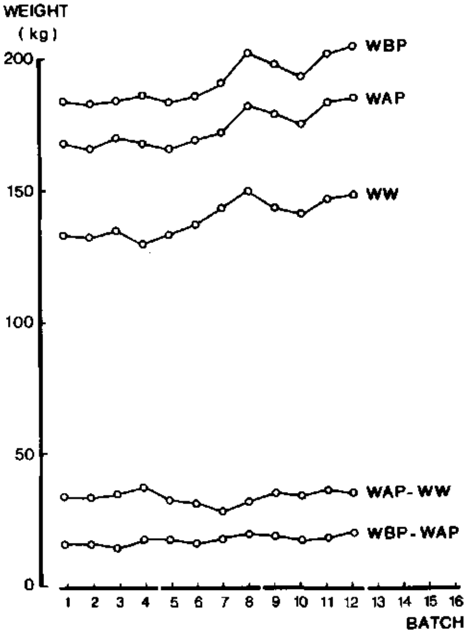


Fig. 4.4 Average weight for each batch just before and after parturition, weight at weaning, weight loss around parturition and during the suckling period.

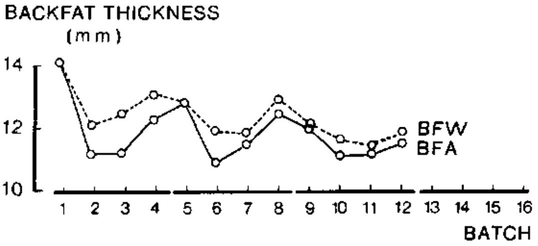


Fig. 4.5. Average backfat thickness at a fixed age (186 d) and weight (~100 kg) for each batch.

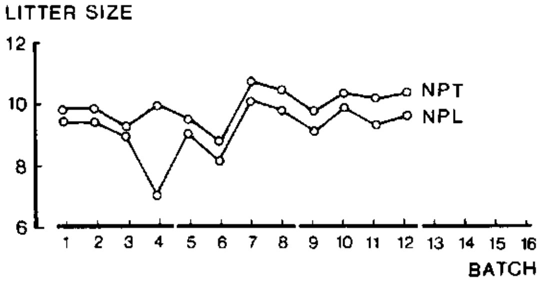


Fig. 4.6. Average number of piglets born alive and total number of piglets born for each batch.

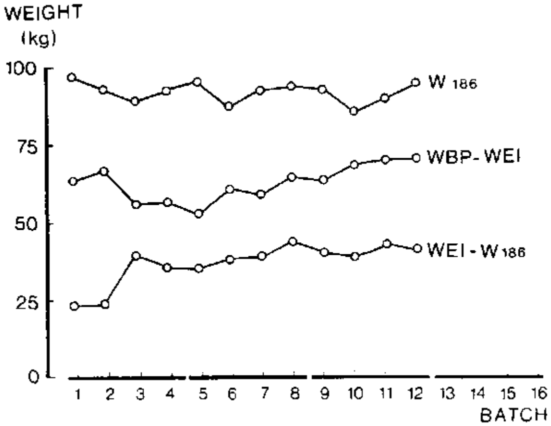


Fig. 4.7. Average body weight at 186 days of age and weight increase to the end of the insemination period and just before parturition for each batch.

Average increase of weight from 186 days of age to the end of the insemination period (WEI-W186) was calculated for all gilts present at the end of the insemination period and for all gilts producing a litter. The weight increase for the gilts which produced a litter did not differ from that for the total population. The tendency mentioned was caused by differences between generations in weight increase from 186 days of age until the end of the insemination period (29.5, 38.1 and 40.5 kg) and in weight increase from the end of the insemination period until one day before parturition (61.3, 58.3 and 67.7 kg) as can be seen in figure 4.7. Backfat thickness of the first batch was surprisingly high. The number of piglets born dead (incl. mummified piglets) was very high in the fourth batch, which coincided with a low proportion of gilts that came on heat. A disease may have been involved although veterinarian inspection did not reveal the cause.

4.2 Correlation between variables.

Correlation coefficients between variables were calculated within batches and pooled. Coefficients are given in table 4.4.

Table 4.4 Correlation coefficients between variables, calculated within batches and pooled.

	WO	W35	W56	W74	W186	WIN	WBP	BFA	BFW	G0-35d	G35-56d	G25-100k	G70k-IN	AFO
35	0.35**													
56	0.29**	0.81**												
74	0.19**	0.55**	0.65**											
186	0.21**	0.38**	0.49**	0.69**										
IN	0.28**	0.33**	0.38**	0.51**	0.83**									
BP	0.23**	0.33**	0.32**	0.32**	0.62**	0.81**								
FA	-0.02	0.12	0.25**	0.40**	0.63**	0.48**	0.32**							
FW	-0.17**	-0.08	0.01	0.10*	0.22**	0.17**	0.09	0.81**						
0-35d	0.21**	0.99**	0.80**	0.55**	0.36**	0.30**	0.31**	0.13*	-0.06					
35-56d	0.16**	0.41**	0.87**	0.54**	0.44**	0.31**	0.21**	0.28**	0.08	0.40**				
25-100k	0.15**	0.12	0.19**	0.24**	0.81**	0.79**	0.65**	0.53**	0.22**	0.10	0.20**			
70k-IN	0.20**	0.03	-0.03	-0.14**	0.17**	0.55**	0.57**	0.09	0.04	0.01	-0.07	0.47**		
FO	0.00	0.04	0.02	0.14**	0.01	0.01	0.02	-0.04	-0.06	-0.01	0.05	-0.10	-0.14**	
PT	-0.04	0.01	-0.04	0.09	0.12	0.12	0.29**	0.09	0.06	0.02	-0.07	0.08	0.03	-0.03

= $p < 0.05$
** = $p < 0.01$

Correlations between weights were, as expected, positive and stronger as weights were further apart in time. In general correlation coefficients between weights and growth were positive and larger as more auto correlation was involved (for instance correlation between W35 and G0-35d). Correlations between weight up to an age of 186 days and growth from 70 kg body weight to the end of the insemination period were weak. Growth before and after 70 kg body weight were hardly related (correlation coefficient between age at 70 kg and growth from 70 kg to the end of the insemination period was -0.03). The relations of weights from 74 days of age up to parturition and growth with backfat thickness were positive and more pronounced for backfat measured at a fixed age than at a fixed weight (correlation coefficients with W186 were 0.63 and 0.22 respectively and with G25-100k 0.53 and 0.22 respectively). Only weight before parturition was markedly related to total number of piglets born (r = 0.29).

Correlation between batches may differ from pooled correlation within batches. This causes a difference between the overall and within batches correlation coefficient only if batch means vary substantially. Cases in which this difference was equal to or greater than 0.05 are presented in table 4.5.

Table 4.5 Correlation coefficients within and between batches, and the overall correlations.

Variables		within batches	correlations between batches	overall
WIN	W35	0.33**	-0.70**	0.25**
WIN	W56	0.38**	-0.57	0.30**
WIN	W186	0.83**	0.27	0.76**
WIN	G0-35D	0.30**	-0.74*	0.21**
WIN	G35-56D	0.31**	-0.29	0.25**
WIN	G25-100k	0.79**	0.17	0.70**
WBP	W35	0.33**	-0.38	0.25**
WBP	W56	0.32**	-0.92**	0.15*
WBP	W74	0.32**	-0.11	0.22**
WBP	W186	0.62**	-0.13	0.46**
WBP	BFA	0.32**	-0.19	0.14*
WBP	BFW	0.09	-0.41	-0.07
WBP	G0-35D	0.31**	-0.43	0.22**
WBP	G35-56D	0.21**	-0.84*	0.02
WBP	G25-100k	0.65**	0.01	0.51**
G25-100k	W56	0.19**	-0.56	0.10*
G25-100k	W74	0.24**	-0.45	0.15*
G25-100k	G35-56D	0.20**	-0.39	0.11*
G70k-IN	W56	-0.03	-0.78*	-0.10
G70k-IN	G0-35D	0.01	-0.56	-0.04
G70k-IN	G25-100k	0.47**	0.09	0.42**
AFO	W186	0.01	-0.76**	-0.17**
AFO	BFA	-0.04	-0.64**	-0.22**
AFO	BFW	-0.06	-0.57	-0.20**
AFO	G25-100k	-0.10*	-0.72**	-0.28**

* = $p < 0.05$
** = $p < 0.01$

Pooled correlation coefficients within batches between weight at insemination or weight before parturition and weight or growth earlier in life were positive while those between batches tended to be smaller or even negative. Within batches there was no, or a very weak, negative relation between age at first oestrus and weight at 186 days of age, backfat thickness and growth from 25 to 100 kg. A few cases are illustrated in figure 4.8. The negative regression coefficient of age at first oestrus to weight at an age of 186 days between batch means was not caused by batch 1. This batch combined an exceptionally low age at first oestrus with a high weight at 186 days (fig. 4.8 A). The negative relation in batch means between backfat thickness at a fixed age and age at first oestrus was, to a large extend, caused by the first batch (fig. 4.8 B). This batch was also responsible for the

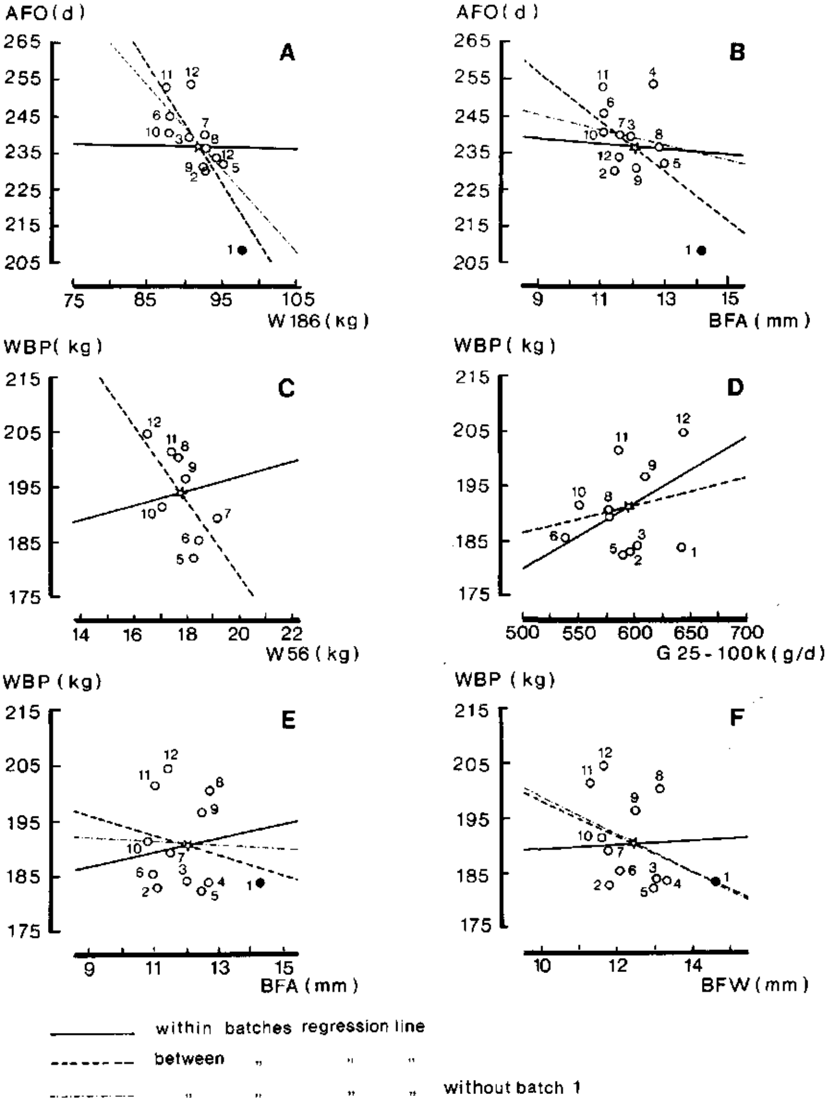


Fig. 4.8 Relations within and between batches of: A. weight at an age of 186 days to age at first oestrus; B. backfat thickness at a fixed age (186 d) to age at first oestrus; C. growth from 25 to 100 kg to weight before parturition; D. weight at an age of 56 days to weight before parturition; E. backfat thickness at a fixed age (∿186 d) to weight before parturition; F. backfat thickness at a fixed weight (∿100 kg) to weight before parturition.

negative relation in batch means between backfat thickness at a fixed age and weight before parturition (fig. 4.8 E).

Pooled correlation coefficients within batches were also calculated making use only of data from gilts which had produced a litter. Deviations from the coefficients presented in table 4.4 were small and always equal to or less than 0.10.

4.3 Variables measured from birth to 56 days of age

4.3.1 Weight and growth

The number of standardized litters, the number of piglets born (live + dead) and the number of piglets alive at 56 days of age of generations 2, 3 and 4 are given in table 4.6.

Table 4.6 Number of standardized litters and piglets.

	Generation		
	2	3	4
Number of litters	72	66	102
Number of piglets born	696	663	1068
Number of piglets alive at 56 days	549	552	828

Birth weight of piglets born and of those alive at 56 days of age (W0b and W0s) were analysed. Other weights and growth to 56 days were analysed making use of dat of surviving piglets only. Data of individual piglets were analysed according to model III (W0b, W0s) or III with birth weight as a covariable (W21, W35, W56, G0-35d, G35-56d).

The main purpose of these analyses was to compare the variance within litters with that between litters in generations 2, 3 and 4 with standardization levels of 8, 6 or 12 and 8 or 9 respectively and the relation of birth weight to growth from birth t days of age. The litter effect was very significant in all cases ($p < 0.01$). This effect was quantified by the intra class correlation (litter variance component divided by the litter plus error variance component). The standardization level was included in the model for analysing data of piglets of generation 3. Intra class correlations for generations 2, 3 and 4 were very similar. The averages are given in table 4.7. Differences between litters accounted for 1/3 of the total variance of weight and growth to 56 days of age. Birth weight was included in mode III. Within litter regression coefficients were very similar for the 3 generations The averages are given in table 4.7. Ignoring the litter effect resulted in within batch regression coefficients which are also given in table 4.7. There was a positive relation ($p < 0.01$) within litters between birth weight and growth from birth up to 56 days of age. This highly significant relation implies an increase of weight at an age of 56 days of 560 g for a 100 g increase in birth weight. Regression coefficients within batches were slightly lower.

able 4.7 The litter intra class correlation for weights and growth up to 56 days of age and the relation of birth weight to weight and growth up to 56 days of age (model III).

ariable (y)	intra class correlation	$b_{y,\ birthweight}$ within litters	within batches
eight			
W0b	0.32		
W0s	0.35		
W21	0.31	2.19	2.12
W35	0.31	3.23	2.96
W56	0.30	5.63	4.98
rowth			
G0-35d	0.31	64	56
G35-56d	0.34	114	96

The effect of standardization level was estimated in three ways. Data of individual piglets of generation 3 were analysed according to models IIIa (birth weight) or IIIa with birth weight as a covariable. Data of individual gilts of generations 2 and 3 which were selected to be reared were analysed according to model I. Litter means of generations 2, 3 and 4 were also analysed according to model I. The significance levels of the generation, period and generation * period interaction effects are given in table 4.8 while least squares means for generations and periods are given in appendix 3.

Table 4.8 The significance levels of the generation, period and generation by period interaction effects for average weights and growth up to 56 days of age (model IIIa).

Variable	generation	period	generation by period
Weight			
AW0b	0.00	0.26	0.36
AW0s	0.00	0.22	0.23
AW21	0.00	0.00	0.01
AW35	0.07	0.00	0.10
AW56	0.00	0.02	0.00
Growth			
AG0-35d	0.07	0.00	0.10
AG35-56d	0.00	0.12	0.04

Birth weight of second generation litters were smaller than those of third and fourth. Growth up to 56 days of age varied between batches. Weight at 56 days decreased from generation 2 to 4. Weaning weights of piglets born in August and November (periods 2 and 3) tended to be higher compared with February and May births.

Least squares means for the high and low standardization level, the difference between them, and the level of significance and the residual standard deviation ar given in tables 4.9 a, b and c respectively.

Table 4.9 Least squares means for the high and low standardization level, the difference between them, and the level of significance and the error standard deviation of growth and weight up to 56 days of age.

a. Data of individual piglets of generation 3 (model IIIa).

	Least squares means				
	STL_H	STL_L	$STL_{(H-L)}$	P	r.s.d.
Weight (kg)					
W0b	1.31	1.33	-0.02	0.65	0.22
W0s	1.36	1.38	-0.02	0.60	0.19
W21	5.00	6.30	-1.30	0.00	0.65
W35	8.38	10.58	-2.20	0.00	1.21
W56	15.77	18.74	-2.97	0.00	2.64
Growth (g/d)					
G0-35d	199	262	-63	0.00	34
G35-56d	351	388	-37	0.07	84

b. Data of gilts which were selected to be reared (data of gilts of generations 2 and 3 were used; model I).

	Least squares means				
	STL_H	STL_L	$STL_{(H-L)}$	P	r.s.d.
Weight (kg)					
W0s	1.40	1.37	+0.03	0.36	0.22
W21	5.07	6.20	-1.13	0.00	0.70
W35	8.61	10.45	-1.84	0.00	1.24
W56	16.38	18.44	-2.06	0.00	2.55
Growth (g/d)					
G0-35d	207	260	-53	0.00	35
G35-56d	370	380	-10	0.40	84

c. Litter means (data of litters of generations 2, 3 and 4 were used; model I).

	Least squares means				
	STL_H	STL_L	$STL_{H-L)}$	P	r.s.d.
Weight (kg)					
AW0b	1.34	1.37	-0.03	0.43	0.17
AW0s	1.38	1.40	-0.02	0.66	0.15
AW21	4.95	6.28	-1.33	0.00	0.51
AW35	8.33	10.55	-2.22	0.00	0.90
AW56	15.76	18.62	-2.86	0.00	1.83
Growth (g/d)					
AG0-35d	198	262	-64	0.00	26
AG0-56d	353	383	-30	0.04	61

Piglets raised in large as compared to small litters grew more slowly during the suckling period and, though the difference was less pronounced, between 35 and 56 days of age (tables 4.9 a and c). This resulted in weight differences at weaning and at 56 days of age of 2.2 and 2.9 kg respectively. The number of piglets of generation 3, alive at 56 days of age, was 552; 287 gilts and 265 castrated males.

92 Gilts were selected to be reared. Those gilts showed smaller weight differences between the two standardization levels at 35 and 56 days of 1.8 and 2.1 kg respectively (table 4.9 b).

4.3.2 Milk consumption, creep feed intake and relations with growth

Milk consumption of 66 litters of generation 3 was measured at ca. 10 and ca. 30 days after birth.

At day 10 a litter failed to suckle only once. At day 30 this occured 9 times (3% of the sucklings at day 30).

Milk consumption on day 30 at the second, third and fourth sucklings of 6 litters which failed to suckle at the first attempt was compared with the corresponding data from litters which did suckle at the first opportunity. Taking the period and standardization level effect into account, the increase in milk consumption after such a failure averaged 23% at the second, third and fourth sucklings. Milk consumption per 240 minutes period was calculated making use of this information.

Milk consumption and creep feed intake from 21 to 35 days of age expressed per litter and per piglet, average weights and growth per litter, and weight of the mother after parturition and at weaning were analysed according to model IIb. Results are given in table 4.10.

Table 4.10 Influence of period and standardization level upon litter traits from birth up to 56 days of age, residual standard deviation and R² (piglets of generation 3; sows of generation 2).

Trait	Least squares means			P		r.s.d.	R²
	STL_H	STL_L	$STL_{(H-L)}$	STL	Period		
Weight (kg)							
AW0s	1.38	1.40	-0.02	0.62	0.17	0.13	0.08
AW21	4.99	6.36	-1.37	0.00	0.05	0.51	0.68
AW35	8.38	10.64	-2.26	0.00	0.20	0.96	0.62
AW56	15.84	18.76	-2.92	0.00	0.54	2.19	0.35
Growth (g/d)							
AG0-21d	171	235	-64	0.00	0.02	23	0.71
AG21-35d	242	305	-63	0.00	0.47	48	0.34
AG35-56d	354	386	-32	0.10	0.13	78	0.13
Creep feed intake (kg)							
CFL21-35	13.80	6.16	7.63	0.00	0.12	5.63	0.37
CFP21-35	1.22	1.09	0.13	0.41	0.27	0.64	0.07
CFL35-56	135.8	88.5	47.3	0.00	0.18	30.2	0.43
CFP35-56	12.3	15.4	3.0	0.04	0.40	4.0	0.16
Milk consumption (g/240 min)							
MLT10	1000	706	293	0.00	0.27	175	0.45
MLT30	910	667	243	0.00	0.05	169	0.40
MPT10	89	122	-32	0.00	0.13	18	0.49
MPT30	82	116	-34	0.00	0.25	23	0.40
MLTS	955	686	268	0.00	0.16	142	0.51
MPTS	86	119	-33	0.00	0.28	17	0.54
Sow weight (kg)							
WAP	172.7	171.8	0.9	0.74	0.00	11.3	0.20
WW	137.5	144.6	-7.2	0.01	0.00	10.7	0.31
WAP-WW	35.2	27.1	8.1	0.00	0.36	7.9	0.25

Weight after parturition differed significantly between periods but there were no significant differences in weight change from parturition to weaning. The influenc of standardization level upon growth from birth to weaning and consequently upon weight at weaning was highly significant. Piglets raised at a high standardization level showed a lower growth rate, lower weaning weight, higher creep feed intake per piglet from 21 to 35 days after birth (not significant) and a lower milk consumption per piglet compared with those raised at a low level. Mothers nursing large litters produced more milk and lost more weight from parturition to weaning. Traits of piglets and sows mentioned in table 4.10 were also analysed according to model IIb in which the covariable was litter size (number of piglets born live or dead). Only the influence of litter size upon birth weight (p = 0.003; b = 0.020 kg/piglet) and weight at 21 days (p = 0.08; b = 0.050 kg/piglet) was significant. Suckling frequency at days 10 and 30 was analysed according to model IIb. No significant differences between the high and low standardization level were presen Suckling frequencies at those levels were 31.4 and 30.7 at day 10 and 26.1 and 25.7 at day 30.

Average growth per piglet was analysed according to model IIb in which the covariables were weight of the mother after parturition, average weight at birth, creep feed intake per piglet from 21 to 35 days after birth, milk consumption per piglet and stability of the teat order (TOSA). Correlations between those covariables, calculated within periods and pooled are given for the high and low standardization level in table 4.11.

Table 4.11 Correlation coefficients between traits which influence growth of piglets during the suckling period (above the diagonal at the high and below the diagonal at the low standardization level).

	WAP	TOSA	AWOs	MPT10	MPT30	MPTS	CFP21-35
Weight of sow after parturition (WAP)		-0.19	-0.10	0.16	0.01	0.10	-0.23
Teat order litter score (TOSA)	0.03		-0.17	-0.16	-0.01	-0.10	0.12
Birth weight (AWOs)	0.10	0.40**		-0.01	-0.20	-0.12	0.32*
Milk consumption (MPT10)	0.04	0.23^{+}	0.19		0.39*	0.84**	-0.21
(MPT30)	0.05	0.03	0.35*	0.15		0.82**	-0.19
(MPTS)	0.06	0.14	0.37*	0.64**	0.86**		-0.17
Creep feed intake (CFP21-35)	0.04	0.16	-0.07	-0.12	-0.28^{+}	-0.28^{+}	

$^{+}$ = $p < 0.10$
* = $p < 0.05$
** = $p < 0.01$

Correlations between weight of the sow, teat order litter score, milk consumption and creep feed intake were small to moderate. At the high standardization level teat order litter score, average birth weight and milk consumption per piglet at day 10 were negatively related while they were positively related at the low level The correlation between average birth weight and creep feed intake per piglet from 21 to 35 days of age was positive at the high but negative at the low standardization level. Because of these differences, average growth per piglet was also analysed separately for the two standardization levels. Results are given in table 4.12.

Table 4.12 Relation of growth of piglets during the suckling period to weight of the sow, teat order litter score, birth weight, milk consumption and creep feed intake (model IIb for analyses 1 to 11; model IIb without STL-effect for analyses 12 and 13.

y-variable: analysis number	covariables	AG0-21d (g/d)			AG21-35d (g/d)			AG0-35d (g/d)		
		b_{yx}	P	R²	b_{yx}	P	R²	b_{yx}	P	R²
1	WAP(kg)	0.50	0.05	0.73	0.35	0.52	0.34	0.45	0.14	0.64
2	TOSA	-2.15	0.49	0.71	0.53	0.99	0.34	-0.99	0.79	0.63
3	AWOs (kg)	26.8	0.23	0.71	21.7	0.65	0.34	25.0	0.34	0.63
4	MPT10 (g)	0.71	0.00	0.80	0.02	0.99	0.34	0.43	0.02	0.66
5	MPT30 (g)	0.38	0.00	0.75	-0.12	0.66	0.34	0.18	0.21	0.64
6	MPTS (g)	0.81	0.00	0.81	-0.10	0.78	0.34	0.44	0.03	0.66
7	CFP21-35 (kg)	2.6	0.57	0.71	63.2	0.00	0.81	26.9	0.00	0.78
8	MPT10 (g) CFP21-35 (kg)	0.74 6.3	0.00 0.10	0.81	0.41 65.2	0.02 0.00	0.83	0.61 29.9	0.00 0.00	0.85
9	MPT30 (g) CFP21-35 (kg)	0.44 7.2	0.00 0.10	0.76	0.42 67.5	0.00 0.00	0.83	0.43 31.4	0.00 0.00	0.83
10	MPTS (g) CFP21-35 (kg)	0.92 9.7	0.00 0.01	0.83	0.68 68.4	0.00 0.00	0.84	0.83 33.3	0.00 0.00	0.87
11	WAP (kg) TOSA WOs (kg) MPTS (g) CFP21-35 (kg)	0.23 -3.15 4.6 0.89 10.1	0.27 0.20 0.80 0.00 0.01	0.84	0.23 -5.71 -37.3 0.73 71.2	0.40 0.08 0.12 0.00 0.00	0.86	0.23 -4.08 -12.1 0.83 34.6	0.20 0.06 0.44 0.00 0.00	0.89
12*	WAP (kg) TOSA WOs (kg) MPTS (g) CFP21-35 (kg)	0.46 -4.36 6.0 0.96 13.66	0.15 0.15 0.85 0.00 0.03	0.63	0.03 -8.73 -72.3 1.06 72.46	0.99 0.02 0.07 0.00 0.00	0.84	0.30 -6.00 -24.6 1.00 37.16	0.29 0.03 0.40 0.00 0.00	0.76
13**	WAP (kg) TOSA WOs (kg) MPTS (g) CFP21-35 (kg)	0.08 2.04 -9.1 0.82 7.67	0.78 0.69 0.73 0.00 0.17	0.57	0.34 -2.51 -17.6 0.38 68.97	0.40 0.72 0.63 0.22 0.00	0.82	0.18 0.37 -12.5 0.64 32.27	0.46 0.99 0.58 0.00 0.00	0.73

* Within the high standardization level

**Within the low standardization level

Growth from birth to weaning was not related to the stability of the teat order and birth weight. The positive relation between weight of the sow after parturition and growth of the piglets from birth to 21 days of age was because of the relation of weight after parturition to milk and creep feed consumption (comparison of first and tenth analyses of table 4.12). Growth from birth to 21 days of age was strongly related to milk consumption (MPT10, MPTS and to a lesser extent MPT30). Growth from 21-35 days of age was not related to milk consumption but very strongly to creep feed intake per piglet. Multiple regression analysis showed a positive relation between growth from 21 to 35 days and milk consumption at a fixed level of creep feed intake. This was caused by the negative relation between creep feed and milk consumption per piglet. An increase of one residual standard deviation of milk consumption per piglet at day 10 (r.s.d. of MPT10 = 18 g; table 4.11) resulted in an increase of growth from birth to 21 days of 13 g/d (4th analysis). An increase of one residual standard deviation of milk consumption per piglet (r.s.d. of MPTS = 17 g) and creep feed intake (r.s.d. of CFP21-35 = 0.64 kg) resulted in an increase of growth from 21 to 35 days of 12 and 44 g/d respectively (10th analysis Analyses per standardization level (12th and 13th analysis) revealed some differences between the two levels. The multiple regression coefficient of growth with the score for stability of the teat order was negative at the high level and close to zero at the low level. Milk consumption was more strongly positively related to growth from 21 to 35 days at the high by comparison with the low standardization level.

Weight loss from parturition to weaning was analysed according to model IIb in which the covariables were weight after parturition, milk consumption per litter and average growth per day from birth to weaning.

Significant multiple regression coefficients (table 4.13) showed that a higher weight loss from parturition to weaning coincided with a higher weight after parturition, a higher milk consumption per litter and a higher growth of the piglet

Table 4.13 Influence of weight after parturition, milk consumption of the litter and average growth of the litter from birth to weaning upon weight loss of the sow during the suckling period (y-variable).

Analysis		estimate	P	Analysis		estimate	P
1. STL(H-L)	(kg)	7.2	0.02	2. STL(H-L)	(kg)	1.9	0.42
$b_{y,WAP}$	(kg/kg)	0.19	0.01	$b_{y,WAP}$	(kg/kg)	0.22	0.01
$b_{y,MLTS}$	(kg/g)	0.021	0.00	$b_{y,MLTS}$	(kg/g)	0.022	0.00
$b_{y,AG0-35}$	(kg/g)	0.076	0.02				
R^2		0.55		R^2		0.50	

Weight after parturition and milk consumption of the litter directly influenced weight loss of the sow. The relation to growth of the piglets indicates that factors other than weight of the sow and milk consumption of the litter, which influence growth of the piglets, are determined by the sow. Correction for weight after parturition and milk consumption of the litter reduced the standardization effect upon weight loss from 8.1 (table 4.10) to 1.9 kg.

Thus the higher weight loss of sows nursing a large litter was to a great extent caused by the higher milk production as no significant difference in weight after parturition existed between sows nursing a small or large litter.

4.3.3 Teat order

At the low standardization level several teats were not occupied. Those teats regressed within a week. Teat order of the piglets was recorded at approximately 10 days after birth. The average number of piglets which suckle at a specific teat is given in table 4.14. No distinction has been made between the left and right teats. The maximum number of piglets suckling at a specific pair of teats is two.

Table 4.14 The average number of piglets which suckle at a specific pair of teats for litters standardized at a high or low level.

teat number	1	2	3	4	5	6	7	8	1-8
STL = H	1.91	1.78	1.53	1.66	1.50	1.56	1.00	0.09	11.03
STL = L	1.29	1.21	1.18	0.76	0.35	0.65	0.32	0.06	5.82

The piglets showed a preference for the anterior teats. At the low standardization level it would have been possible for the piglets to suckle at the first three pairs of teats. Only 63% of those piglets suckled at the three anterior pairs of teats. At the high standardization level 47% of the piglets suckled at the three anterior pairs of teats while this could have been 54%.

The stability of the teat order was calculated in two ways. The first score (TOSA) combines several features of stability while the second (TOSB) is determined by the number of piglets which suckle a teat 3 times, twice or only once. The correlation coefficient between TOSA and TOSB is 0.85 at both the high and low standardization levels. Frequency distributions are given in figure 4.9 for TOSA and TOSB at the high and low standardization levels. Stability of the teat order is higher at the high standardization level.

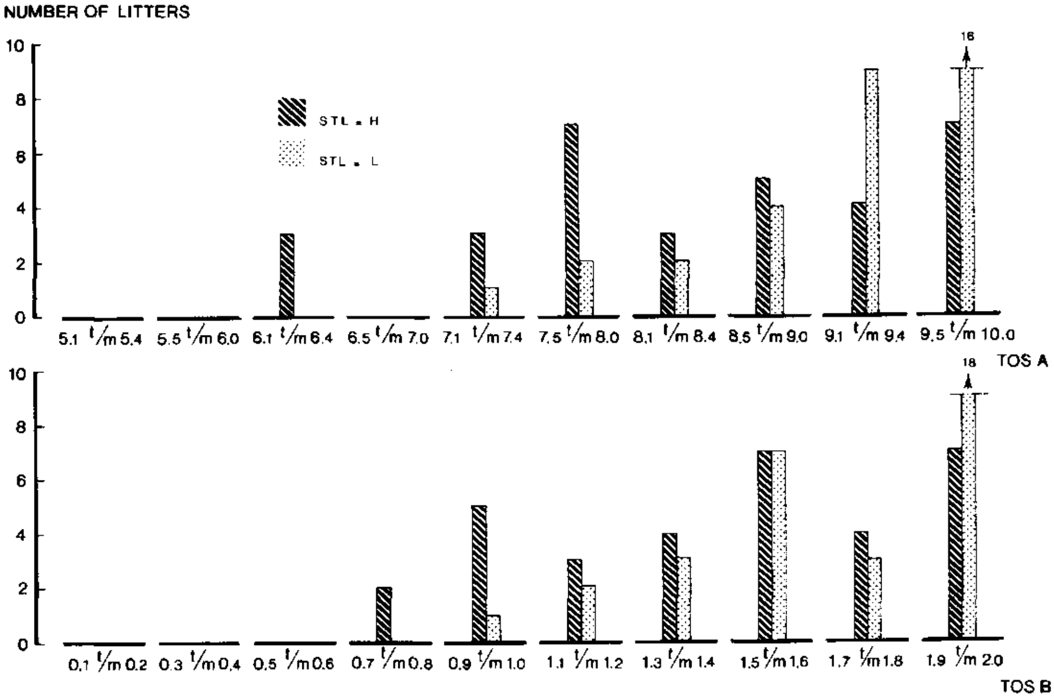


Fig. 4.9 Frequency distribution of stability of the teat order (TOSA and TOSB) for high and low standardization level litters.

4.4 Variables measured from 74 days of age up to parturition

4.4.1 Growth and backfat thickness

Growth, weights and backfat depth measured during the rearing period were analysed according to models I and II.

Generation and period least squares means, regression coefficients with age and weight and the significance level of generation, period, generation * period interaction effects and covariable(s) are given in appendix 4.

Differences between batches were very significant. Weight at an average age of 214 days (least squares mean) of the fifth batch was minimal (101 kg) and maximal for the twelfth batch (113 kg). Batch means for weight before parturition varied betwe 183 kg (batch 5) and 206 kg (batch 12) while for backfat thickness means varied between 11.5 mm (batch 11) and 14.0 mm (batch 1). Weight increase from W74 to W214 was lowest in period 2 so gilts born in August had a low growth rate from November to February. Weight before parturition was highest for gilts born in February. Weight at a particular weighing was related to age of the gilt at that time.

The age range within a batch was 20 days. Regression coefficients were of the same order as growth per day. For instance the regression coefficient of weight to age at approx. 214 days equalled 0.629 kg/d while growth from 25 to 100 kg equalled 597 g/d. Growth per day from 25 to 100 kg body weight was negatively related to the age at 25 kg while growth per day from 70 kg to insemination was not significantly related to age at 70 kg. Growth from insemination to parturition was also unrelated to age at insemination. The relation between weight at insemination and growth from insemination to parturition was negative. Animals growing fast early in life (A25k low) grew fast afterwards (G25-100k high) but animals that grew fast up to insemination (WIN high) grew more slowly afterwards (WAP-WIN low). Backfat thickness measured at approximately a fixed age was influenced by weight at measurement while backfat thickness measured at approximately a fixed weight of 100 kg was influenced by both age and weight. At a fixed weight backfat thickness decreased as age increased and at a fixed age backfat thickness increased as weight increased. Fast growing gilts deposited more backfat than slow growing gilts.

The relations between backfat and growth variables were examined in more detail by analysing growth per day, weights and weight increase by model I on an individual and pen mean basis. Pen means were only calculated if backfat measurement data of the four gilts put together at the beginning of the rearing period were available. So death or culling of one gilt resulted in eliminating the data from all animals of that pen. Results are given in table 4.15. Data of generation-3 gilts were analysed according to model IIb in which regression was over or within the standardization level subclasses and results are also given in table 4.15. Individual data of 477 gilts and means of 101 pens were used. At the individual level all relations between growth variables and backfat thickness were positive. One standard deviation unit of weight at the age of 186 days coincided with 1.24 mm backfat (BFA). The relation between growth and backfat thickness at a fixed weight of approximately 100 kg was less strong. One standard deviation unit of growth per day from 25 to 100 kg coincided with 0.39 mm backfat (BFW).

At the pen mean as compared to the individual level the regression coefficients were approximately 35% smaller.

There tended to be a difference between regression coefficient at the high as opposed to the low standardization level, regression coefficients tending to be higher at the high level.

Least squares means for the high and low standardization level and for halothane non-susceptible (negative) and susceptible (positive) gilts are given in appendix 5. Data from batches 6 to 12 were used. Interaction of halothane susceptibility and

Table 4.15 Relation between growth and backfat thickness.

y-variable		covariable(s) in the model (x)		individual data		pen means	
				b_{yx}	P	b_{yx}	P
model I							
G25-100k	(g/d)	BFW	(mm)	9.557	0.00	5.737	0.22
		A25k	(d)	-2.320	0.00	-1.327	0.18
G25-100k	(g/d)	BFW	(mm)	9.936	0.00	5.915	0.21
W186-W74	(kg)	BFA	(mm)	1.386	0.00	0.381	0.07
		AW74	(d)	-0.160	0.01	-0.060	0.38
		W74	(kg)	0.299	0.00	0.204	0.03
W186-W74	(kg)	BFA	(mm)	1.485	0.00	0.605	0.00
W186	(kg)	BFA	(mm)	1.863	0.00	1.132	0.00
		AW186	(d)	0.471	0.00	0.592	0.00
W186	(kg)	BFA	(mm)	2.226	0.00	2.248	0.00
W100k	(kg)	BFW	(mm)	0.501	0.00	0.299	0.17
		AW100k	(d)	0.094	0.00	0.118	0.00
W100k	(kg)	BFW	(mm)	0.397	0.00	0.203	0.40
BFA	(mm)	W186	(kg)	0.128	0.00	0.098	0.00
		AW186	(d)	0.022	0.18	0.037	0.23
BFA	(mm)	W186-W74	(kg)	0.150	0.00	0.134	0.01
		AW74	(d)	0.086	0.00	0.092	0.00
BFW	(mm)	W100k	(kg)	0.112	0.00	0.072	0.17
		AW100k	(d)	-0.022	0.00	-0.020	0.16
BFW	(mm)	AW100k	(d)	-0.012	0.01	-0.011	0.37
BFW	(mm)	G25-100k	(g/d)	0.004	0.00	0.003	0.22
		A25k	(d)	-0.005	0.71	-0.002	0.99
BFW	(mm)	G25-100k	(g/d)	0.004	0.00	0.003	0.21
model II							
G25-100k	(g/d)	BFW	(mm)	16.594	0.00	9.219	0.14
		A25k	(d)	-3.120	0.00	-1.873	0.14
G25-100k within STL	(g/d)	BFW mean 1)		16.981	0.00	9.672	0.12
		STL = H 2)		21.772	0.18 3)	14.117	0.47 3)
		STL = L 2)		12.189		5.228	
		A25k mean 1)		-2.790	0.01	-1.467	0.27
		STL = H 2)		-4.543	0.11 3)	-3.193	0.20 3)
		STL = L 2)		-1.036		0.260	

1) mean of two regression coefficients within standardization level

2) regression coefficient within a standardization level

3) difference between the two regression coefficients tested

standardization level was tested in data of batches 9 to 12 (generation 3). Those results are given in appendix 6. The interaction effect was significant for weight at the end of the insemination period. Least squares means for the high and low standardization level are summarized in table 4.16.

Table 4.16 Influence of standardization level upon weight, growth and backfat thickness during the rearing period (*least squares means*) for all gilts (*model II*) and halothane non-susceptible gilts (model II without HAL-effect).

Variable	all gilts		halothane non-susceptible gilts	
	STL_H	STL_L	STL_H	STL_L
Weight (kg)				
W74	23.0	25.8	23.2	25.5
WEI	129.2	130.1	131.3	131.3
WBP	194.7	198.9	197.7	200.8
WAP	177.7	181.4	179.3	182.1
Growth (g/d)				
G25-100k	593	583	614	594
Backfat thickness				
BFA	11.15	10.86	11.94	11.49
BFW	11.55	11.05	12.22	11.62

The influence of standardization level upon weight decreased as gilts grew older. A significant difference at 74 days was not present at day 214. At the end of the insemination period this difference was -0.9 kg; gilts raised at the low standardization level being slightly heavier than those raised at the high level. This difference was zero in halothane non-susceptible gilts. From insemination till one day before parturition this difference increased significantly. Low standardization level gilts were 4.1 kg heavier just before parturition than those at the high level. In halothane non-susceptible gilts this difference was 3.1 kg. The effect of standardization level upon weight was larger in halothane susceptible gilts. At an age of 74 days this difference was 4.4 kg which did not decrease as gilts grew older. Just before parturition the difference was 6.2 kg. The estimate of the standardization level effect in halothane susceptible gilts was not very accurate as only a small number of gilts was involved. At the end of the insemination period 174 gilts of generation 2 were present. 23 Gilts were halothane susceptible.

Growth from 25 to 100 kg was 10 g/d higher for gilts raised at the high compared with the low standardization level. In halothane non-susceptible gilts this difference was 20 g/d (p = 0.03). At a weight of 100 kg the difference in backfat thickness was 0.5 mm.

Halothane negative by comparison with positive gilts grew faster from 25 to 100 kg and deposited more backfat. Difference in weight one day before parturition was 4.9 and just after parturition 2.5 kg. The effect of halothane susceptibility upon growth and backfat thickness was very significant.

4.4.2 Age at first oestrus

Oestrus in gilts was recorded from an average age of 168 days to the end of the 3 weeks insemination period. This period ended at an average age of 268 days. The mean age at first oestrus and the median for each batch are given in table 4.17.

Table 4.17 Mean age at first oestrus and the median for each batch.

Batch	mean(d)	median(d)	Batch	mean(d)	median(d)	Batch	mean(d)	median(d)
1	208	213	5	231	233	9	230	230
2	230	231	6	245	251	10	240	242
3	239	245	7	240	245	11	253	258
4	-	-	8	236	238	12	233	233

Variables which were analysed are: age at first oestrus (AFO), age at first oestrus as a deviation from the batch median (AFOM) and age at first oestrus as a deviation from the median supplemented by values for gilts which did not show first oestrus before the end of the insemination period (AFOMS). AFO was analysed according to models I and II while AFOM and AFOMS were analysed according to models Ia and IIa. The covariables growth per day from 25 to 100 kg and backfat thickness at a fixed weight were in some cases inserted into the models. Generation, period and generation by period interaction effects were always very significant. The cumulative percentage of gilts which showed first oestrus (CPO) per batch is given in figure 4.10.

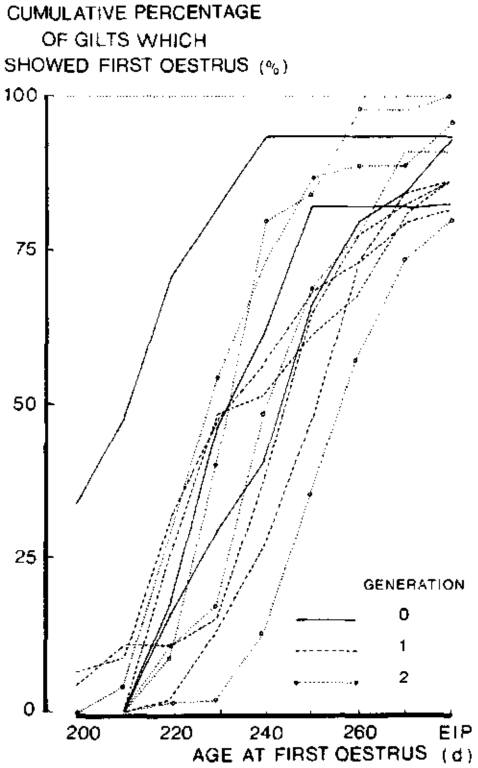


Fig. 4.10 Cumulative percentage of gilts which showed first oestrus for each batch.

At the end of the insemination period this varied between 80 and 100%. No clear relation existed between age at onset of oestrus within a batch and CPO at the end of the insemination period. The correlation between CPO at 220 days and at the end of the insemination period was 0.30 (non significant). The percentage of gilts per batch which showed first oestrus at an age of 240 days varied between 13 and 93. Age at which 50% of the gilts had shown first oestrus varied between 213 and 258 days.

The influence of standardization level upon cumulative percentage of gilts which showed first oestrus is illustrated by figures 4.11 and 4.12.

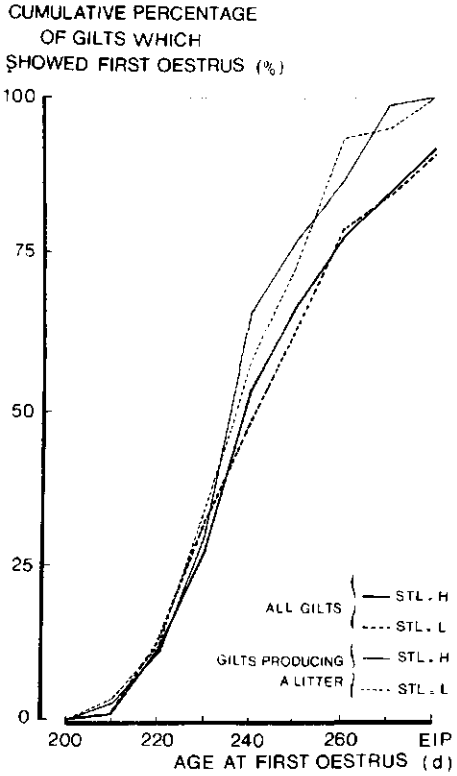


Fig. 4.11 Influence of standardization level upon age at first oestrus.

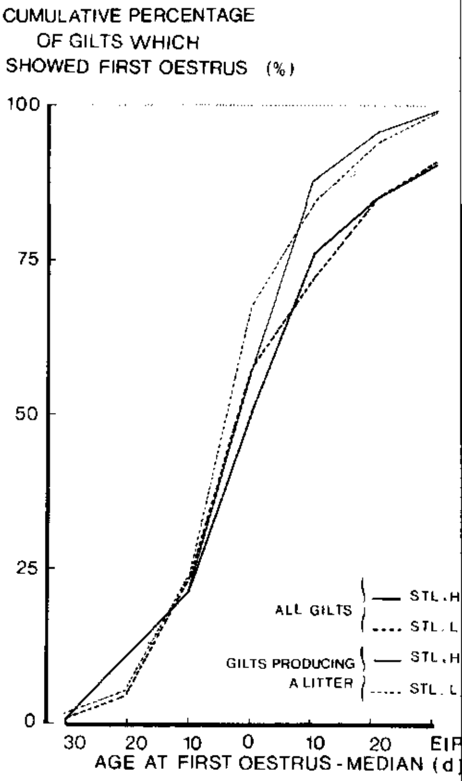
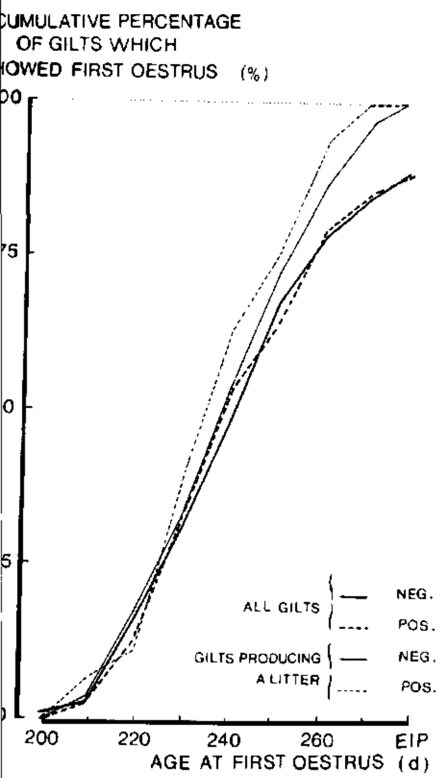


Fig. 4.12 Influence of standardization level upon age at first oestrus expressed as a deviation from the batch median.

In these figures least squares means are given ($\hat{\mu} + \hat{G}e_2 + \widehat{STL}_k$, results from model II for AFO and IIa for AFOM). Data of all gilts present at the end of the insemination period as well as those which produced a litter were analysed. Similarly, the influence of halothane susceptibility is illustrated by figures 4.13 and 4.14 ($\hat{\mu} + \widehat{HAL}$).



ig. 4.13 Influence of halothane susceptibility upon age at first oestrus.

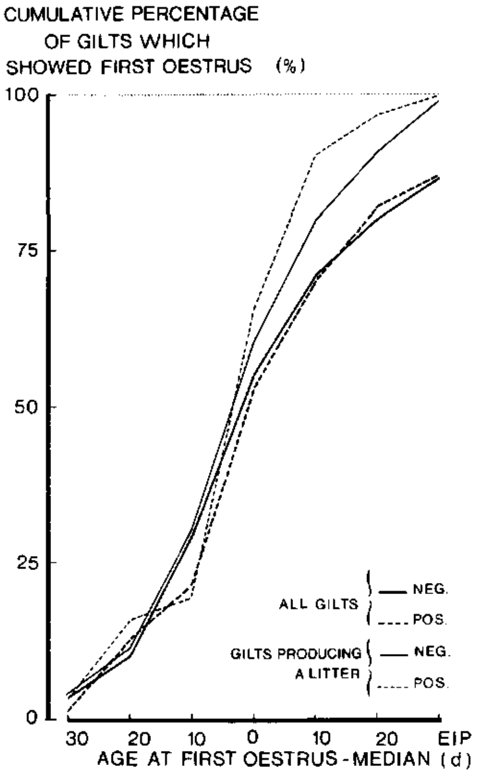


Fig. 4.14 Influence of halothane susceptibility upon age at first oestrus expressed as a deviation from the batch median.

ifferences between the high and low standardization level gilts and between alothane positive and negative pigs for percentage of gilts which came on heat efore a specific moment (age expressed in days or as a deviation from the ppropriate median) were never significant (P > 0.10). Analysis of age at first estrus and age at first oestrus as a deviation from the batch median supplemented y values for gilts which did not show first oestrus revealed no significant ifferences between the two standardization levels or between halothane positive nd negative pigs (table 4.18).

able 4.18 Influence of standardization level and halothane susceptibility upon age at first oestrus (contrasts; models II and IIa).

ariable	STL(H-L) without cov.	with cov.	HAL(neg-pos) without cov.	with cov.
ll gilts				
O (d)	-0.79	-0.18	-2.07	-0.62
OMS (d)	-1.23	0.55	-0.35	0.55
lts which produced a litter				
O (d)	-0.71	-0.31	0.73	2.30
OMS (d)	-0.17	0.21	1.77	2.82

Age at first oestrus may be related to backfat thickness and/or growth. Multiple regression coefficients of backfat thickness at a fixed weight and growth per day from 25 to 100 kg with age at first oestrus (AFO and AFOMS; models II and IIa) are given in table 4.19. Fast growing animals came on heat at an earlier age compared with slower growing animals.

Table 4.19 Regression of age at first oestrus with backfat thickness and growth per day from 25 to 100 kg (multiple regression coefficients)(models II and IIa with covariables).

Animals :	All gilts		Gilts which produced a litter	
covariable:	BFW (mm)	G25-100k(g/d)	BFW (mm)	G25-100k(g/d)
y-variable				
AFO (d)	-0.02	-0.052*	0.09	-0.045*
AFOMS (d)	-0.14	-0.048**	0.05	-0.026

* = $p < 0.05$
** = $p < 0.01$

4.4.3 Insemination results

In total 409 gilts were inseminated. The average conception rate was 71% but varie between batches (table 4.20) in a range of 57 to 79%.

Table 4.20 Conception rate (CR) per batch.

Batch	N	CR(%)	Batch	N	CR(%)	Batch	N	CR(%)
1	38	68	5	35	71	9	42	60
2	31	77	6	33	79	10	38	71
3	34	65	7	35	66	11	37	78
4	20	75	8	23	57	12	43	79
	123	71		126	69		160	72

Conception rate was defined as the percentage of gilts which had farrowed or appeared to be pregnant at the time of slaughtering. Conception rate decreased significantly as the oestrus number at insemination increased (table 4.21, $\chi^2_2 = 5.27$, $p = 0.07$).

Table 4.21 Conception rate (CR) per oestrus number at insemination.

ONI	N	CR(%)
1	139	76
2	144	72
≥3	126	64
	409	71

Conception rate of halothane tested gilts (from batch 6 onwards) is given in table 4.22.

able 4.22 Conception rate for halothane susceptible and non-susceptible gilts for each oestrus number at insemination (batches 6 to 12).

NI	1		2		≥3		total	
AL	neg.	pos.	neg.	pos.	neg.	pos.	neg.	pos.
umber of gilts inseminated	76	20	85	16	46	8	207	44
umber of gilts conceiving	59	13	56	14	29	6	144	33
onception rate (%)	78	65	66	88	63	75	70	75

Conception rates for 207 halothane negative and 44 positive gilts were 70 and 75% respectively which difference was not significant. Conception rate for gilts raised at the high compared with the low standardization level was lower ($\chi_1^2 = 9.13$, $p = 0.00$) when insemination took place at first oestrus and higher ($\chi_1^2 = 1.49$, $p = 0.22$) if gilts were inseminated at second or later oestrus (table 4.23).

able 4.23 Conception rate for gilts raised at high or low standardization level for each oestrus number at insemination (batches 9 to 12).

NI	1		2		≥3		total	
TL	H	L	H	L	H	L	H	L
umber of gilts inseminated	24	31	41	26	17	21	82	78
umber of gilts conceiving	12	28	32	18	13	12	57	58
onception rate (%)	50	90	78	69	76	57	70	74

The overall difference (70-74%) was not significant. This resulted in a lower fraction of high standardization level gilts inseminated at a first oestrus and producing a litter compared with the low level (table 4.24, $\chi_1^2 = 8.25$, $p = 0.00$).

able 4.24 Number of gilts per standardization level and per oestrus number at insemination for all inseminated gilts and gilts which produced a litter (batches 9 to 12).

	All Gilts		Gilts which produced a litter	
TL	H	L	H	L
NI 1	24	31	11	27
≥2	58	47	45	28

The effect of standardization level does not differ significantly between halothane susceptible and non-susceptible gilts (table 4.25).

Table 4.25 Conception rate for halothane susceptible and non susceptible gilts raised at a high or low standardization level (batches 9 to 12).

HAL	negative		positive	
STL	H	L	H	L
number of gilts inseminated	71	68	11	10
number of gilts conceiving	48	50	9	8
conception rate	68	74	82	80

4.4.4 Litter size

Total number of piglets born was analysed according to model I (in which oestrus number at insemination was included) to estimate the differences between generations and groups. Litter size increased as generation number increased (9.56, 9,77 and 10.01). Litters born in May and August were smaller than litters born in November and February (9.41, 9.54 and 10.11, 10.05 respectively). Litter size of gilts of batches 6 to 12 was analysed according to model II (with ONI) to estimate the influence of standardization level after correction for halothane susceptibility. Results are given in table 4.26.

Table 4.26 Influences of generation, period, generation * period, standardization level, oestrus number at insemination and halothane susceptibility upon total number of piglets born (model II, batches 6 to 12; model IIb, batches 9 to 12).

	least squares means (n)		contrast		significance level	
model	II	IIb	II	IIb	II	IIb
Ge					0.79	
Per					0.13	0.19
Ge*Per					0.34	
STL=H	9.31 (56)	9.12 (56)	-0.32	-0.57	0.54	0.30
STL=L	9.63 (55)	9.69 (55)				
ONI=1	8.83 (68)	8.28 (39)	-1.15	-2.24	0.03	0.01
ONI≧2	9.98 (103)	10.52 (73)				
HAL=neg	10.04 (140)	9.89 (96)	1.27	0.98	0.02	0.20
HAL=pos	8.77 (31)	8.91 (15)				
R^2	0.10	0.09				
R.s.d.	2.65	2.73				

A similar analysis was carried out for halothane negative gilts (omitting the factor HAL) as most gilts were halothane non-susceptible. Results are given in table 4.27.

Table 4.27 Influences of generation, period, generation * period, standardization level and oestrus number at insemination upon total number of piglets born of halothane negative gilts (model II, batches 6 to 12; model IIb, batches 9 to 12).

	least squares means (n)		contrast		significance level	
model	II	IIb	II	IIb	II	IIb
Ge					0.77	
Per					0.22	0.30
Ge*Per					0.74	
STL=H	9.79	9.63	-0.48	-0.62	0.39	0.29
STL=L	10.27	10.25				
ONI=1	9.41	8.95	-1.38	-1.98	0.02	0.02
ONI≧2	10.79	10.93				
R^2	0.07	0.07				
R.s.d.	2.61	2.66				

The effect of standardization level was measured in batches 9 to 12. Those data were analysed according to model IIb (table 4.26). Results for halothane non-susceptible gilts only are given in table 4.27. The difference in litter size between gilts raised at the high or low standardization level was -0.32 (model II) or -0.57 (model IIb). This difference was larger for halothane negative gilts only (-0.48 or -0.62). The two models resulted in different estimates for the standardization level effect as more data are involved when model II was used. The estimates of oestrus number at insemination and halothane susceptibility were more accurate in that case.

Halothane susceptibility decreased litter size (-1.28 piglets). Oestrus number at insemination significantly influenced litter size. Analyses showed that the influences of second and third oestrus number at insemination upon litter size were similar. Litters conceived at first oestrus were approximately one piglet smaller than those conceived at second or subsequent oestrus. This difference was very pronounced for the batches 9 to 12 (-2.24 piglets/litter). The interaction between standardization level and oestrus number at insemination was added to models II and IIb to study these two factors in greater detail. Results are given in table 4.28.

Table 4.28 Influence of standardization level by oestrus number at insemination interaction upon total number of piglets born.

		Batches 6 to 12 (ONI included in model II). least squares means	(n)	Batches 9 to 12 (ONI included in model IIb). least squares means	(n)
ONI=1	STL=H	9.16	(11)	8.25	(11)
	STL=L	8.85	(27)	8.46	(27)
ONI≥2	STL=H	9.79	(45)	10.16	(45)
	STL=L	10.41	(28)	10.93	(28)
Significance level of ONI * STL		0.38		0.59	

Standardization level only influenced litter size of gilts inseminated at second or later oestrus. Oestrus after weaning of the first litter was recorded in 104 sows of the third generation. Oestrus of the sows was induced if they did not show oestrus before 21 days after weaning. Five sows were culled for various reasons. Two sows came into heat before 21 days after weaning while no corpora lutea were present at slaughtering. Two sows which had to be induced did not show heat but at slaughtering at day 28 after weaning,corpora lutea were present. So the data from 95 sows were analysed. 56 Sows came into heat spontaneously: 25 out of 56 high standardization level sows and 31 out of 49 low standardization level sows, the difference being not significant.

Weight of the uterus, length of the right + left uterus horn, weight of the ovaries and number of corpora lutea were analysed. Results are given in table 4.29.

Table 4.29 Influences upon number of corpora lutea, weight of ovaries, uterus weight, length of the uterus horns and interval from weaning to oestrus of generation-3 sows after weaning of the first litter.

	Significance levels				estimates				
	Batch	STL	OIND	HAL	μ	STL (H-L)	OIND (sp-ind)**	HAL (neg-pos)	r.s.d.
All sows									
uterus weight (g)	0.78	0.00	0.13	0.02	547	-85	-44	103	131
length of uterus horns (cm)*	0.00	0.10	0.00	0.03	270	-20	-38	41	56
weight of ovaries (g)	0.13	0.41	0.43	0.23	12.2	-0.8	-0.8	1.8	4.6
Sows with induced oestrus									
number of corpora lutea	0.73	0.15		0.43	21.3	-3.9		1.7	8.0
Sows with spontaneaous oestrus									
number of corpora lutea	0.90	0.71		0.99	15.6	0.3		-0.1	2.9
interval weaning to oestrus (d)	0.98	0.26		0.21	9.8	-1.7		-3.5	5.2

* sum of left and right.
** oestrus induction after weaning of the first litter; sp= spontaneous oestrus, ind=induced oestrus.

As the variance of number of corpora lutea was larger for gilts in which oestrus was induced when compared with gilts which came on heat spontaneously, number of corpora lutea was analysed separately for the two groups. The interval from weaning to oestrus was only analysed for gilts with a spontaneous oestrus. Gilts raised at the high as against the low standardization level had a somewhat less developed uterus i.e. lower weight and shorter uterus horns. No differences in weight of the ovaries were detectable. The number of corpora lutea tended to be lower for high than for low standardization level sows after the induction of oestrus. This was not so in sows which came on heat spontaneously.

Halothane susceptible sows had a lower uterus weight and shorter uterus horns than non-susceptible sows. They produced fewer corpora lutea and came later on heat although these differences were not significant.

Relations between litter size and weight at insemination, weight before and after parturition and weight change from insemination to just before or after parturitic were studied according to model I and results are given in table 4.30.

Table 4.30 Regression of litter size (y) to weight at insemination, weight around parturition and weight change from insemination to parturition (model I, with covariable).

Analysis	covariable (x)	b_{yx}	P
1	WIN (kg)	0.0215	0.22
2	WBP (kg)	0.0635	0.00
3	WAP (kg)	-0.0109	0.50
4	WBP-WIN (kg)	0.1415	0.00
5	WAP-WIN (kg)	-0.0938	0.00

Litter size was not related to weight at insemination and weight just after parturition. Gilts carrying larger litters gained more weight from insemination tc just before parturition but they gained less from insemination to just after parturition.

5 DISCUSSION

5.1 Experimental design

Three generations of gilts were reared. The first generation was purchased, the second was raised in litters standardized at 8 piglets while the third generation gilts (batches 9 to 12) were raised in litters of 6 (low) or 12 piglets (high). Thus the effect of the standardization level on production and reproduction traits was measured in gilts of generation three. High and low standardization level gilts were raised by their own mothers. As those mothers were raised in litters standardized at 8 piglets, no grand-maternal influences, as determined by litter size, upon the high and low standardization level gilts were present. The high and low standardization level groups were equalized with respect to the additive genetic value by allotting small as well as large litters at birth to both groups. Average litter size (total number of piglets born) and weight after parturition did not differ significantly between sows raising a large or small litter, the averages being 10.2 and 10.0 piglets and 172.7 and 171.8 kg respectively. Average birth weight of the young was 1.31 and 1.33 kg respectively.

Halothane susceptibility and oestrus number at insemination appeared to be important factors. Gilts of batches 1 to 5 were not tested for halothane susceptibility. This complicated the statistical analysis. As the effect of standardization level was measured in gilts of batches 9 to 12, correction for halothane susceptibility was possible. Oestrus number at insemination was variable as the age at insemination was fixed. It would have been possible to inseminate at a fixed oestrus number but in that case age at insemination would have been more variable.

5.2 Body weight of high and low standardization level gilts from birth to parturition

In figure 5.1 the body weight of gilts in batches 9 to 12 from birth to parturition is given. Overall means were used. The body weight curve from birth to insemination was s-shaped. This pattern was disrupted during pregnancy. The relatively large weight increase during pregnancy may be due to fluids in the genital tract and mammary glands. An increase of blood and energy and protein retention in pregnant compared with non-pregnant gilts may also cause a relatively (to the standard s-shaped curve) large weight increase during pregnancy.

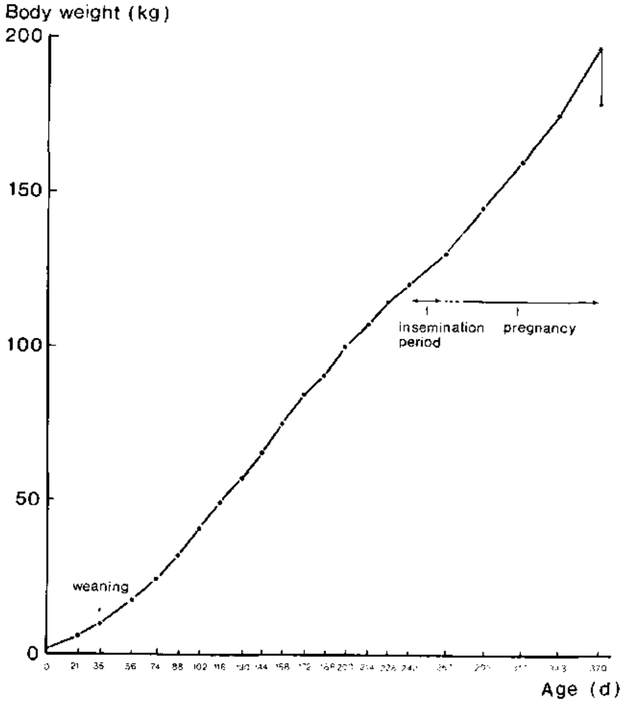


Fig. 5.1 Body weight curve from birth to parturition.

De Wilde (1980) compared pregnant with non-pregnant gilts. Pregnant gilts deposited more protein during pregnancy (4.16 and 3.19 kg respectively). He also reported an increased weight of the empty genital tract, mammary glands and blood. The weight increase of pregnant gilts was 16 kg more than of the non-pregnant gilts. Differences between high and low standardization level gilts are given in figure 5.2. The following five periods were represented in this figure:

1. from birth to 56 days of age
2. from 56 to 200 days of age
3. from 200 days of age to just after the insemination period
4. from just after the insemination period to four weeks before parturition
5. the last four weeks of pregnancy.

The number of animals involved in those periods were 552, 189, 174, 108 and 107 respectively. Data on weights at 56 days of all piglets and of gilts which were selected to be reared were analysed. From day 74 onwards data of all gilts were analysed according to model IIb and data of halothane negative gilts were analysed using this model omitting the HAL-effect. The weight difference increased over the period from birth to 56 days of age (fig. 5.2).

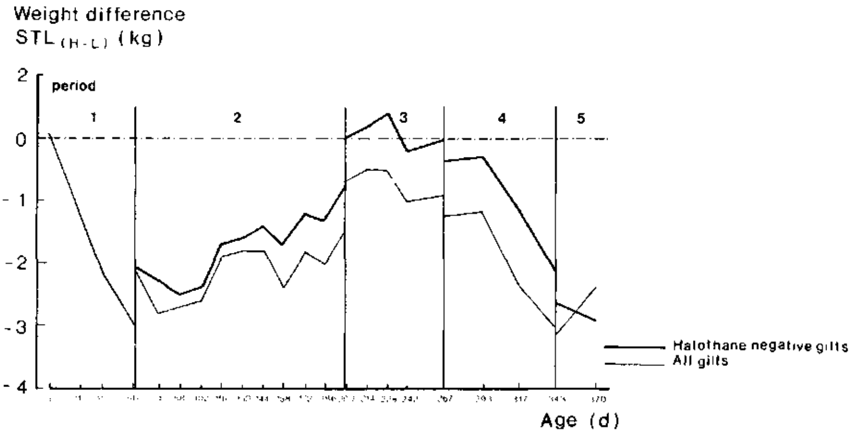


Fig. 5.2 The effect of standardization level on body weight in halothane negative gilts and in all gilts (HAL-effect included in the model).

At the end of this period the weight difference amounted to 17% of the mean. The difference decreased over the period from 56 to 200 days of age. At 200 days a contrast of 1 kg represented not more than 1% of the mean in halothane negative gilts. As ca. 86% of the gilts were halothane negative,estimates obtained by analysing data of those gilts, seemed to be most appropriate. The weight difference between both standardization level groups did not change from 200 days of age to just after insemination and was virtually zero. During pregnancy the weight difference increased. This small difference, relative to body weight, was not significant. The contrast was maintained from 74 days to parturition in halothane positive gilts. Thus using all data and including the halothane susceptibility effect in the model gave different estimates of the standardization effect. An influence of standardization level on weight at 42 or 56 days of age (close to breeding) in mice was reported (table 2.7). Increasing standardization level from 8 to 16 gave a reduction in body weight of ca. 10%. It must be noted that weaning weight in mice is relatively high compared with that in pigs. As a result of this, the weaning weight in mice is relatively close to their adult weight.

It can be concluded that

- the weight difference between both standardization level groups was significant

and substantial at 56 and 74 days of age
- the difference had disappeared at insemination.

These conclusions are in agreement with results obtained by Rutledge (1980). Nelson and Robison (1976) found no reduction in weight differences between both standardization level groups, although they only analysed weight at an age of 140 days.

5.3 Variables measured from birth to 56 days of age

5.3.1 Weight and growth

The variance between litters accounted for ca. 32% of the total variance in weight and growth to 56 days of age (table 4.7). As the litter was the experimental unit for variables as creep feed intake and milk consumption, litter means for weight and growth of the piglets were also calculated and analysed (table 4.9c). Growth of litters from birth to weaning, expressed per piglet, at the high level was reduced by 24% compared with those at the low level. From weaning to 56 days of age this reduction was 8%. This resulted in a 17% decrease in growth from birth to 56 days of age. Nelson and Robison (1976b) observed a reduction of growth from birth to 56 days of 30%. This larger decrease may have been due to the higher age of the piglets at weaning or the higher upper level of standardization (14 piglets) A different housing, feeding and management system may also have caused this difference. A relatively large effect of standardization level on weaning weight in mice was reported. Increasing the standardization level from 8 to 16 reduced the weaning weight (at 3 weeks) by about 35% (table 2.7).

It was not possible to rear all the gilts raised at both standardization levels. The aim was to select about 2 gilts out of each litter. The weaning weight had to be as close to the litter mean as possible. As a result of this selection the weight difference at 56 days of age decreased from -2.97 to -2.06 kg. It would have been better to have reared all the gilts or to have selected the gilts at random.

5.3.2 Milk consumption, creep feed intake and growth

5.3.2.1 Milk consumption and creep feed intake

Milk consumption data of this experiment may be biased because of
- time interval between sucklings of 60 minutes

- weighing procedure
- metabolic and evaporative losses
- weight loss due to urination and defaecation.

Time interval between sucklings was ca. 46 and 56 minutes at both standardization levels at days 9 and 29 of lactation respectively. Milk consumption may be underestimated especially at day 10. As suckling frequency was equal at both standardization levels this does not seriously bias the contrast in milk consumption between the two levels.

Den Hartog et al. (1983) concluded from the literature that measurement 6 times per day(suckling intervals of 1 hour)was long enough to give reliable estimates of milk produced by the sow. In this study milk production was measured 4 times. The intervals between a weighing before and after suckling were 11.5 and 8.9 minutes on average at day 10 and 11.9 and 9.6 minutes at day 30 for high and low standardization level litters. Weight loss of piglets due to metabolism and evaporation depends upon the time interval between weighings and the age and weight of piglets. Den Hartog et al. (1983) derived the relation to age

$$y = 0.443 + 0.019\ A$$

while in these data the relation to weight was (Hermans, 1982)

$$y = 0.406 + 0.079\ W$$

where y = loss in weight due to metabolic rate and evaporation in g per piglet per minute. Weight loss of active pigs was measured.

A = age in days.

W = weight of the piglet in kg.

The correlation coefficient of age with weight was 0.94, so a separation of the effects of age and weight on loss in weight due to metabolic rate and evaporation was not possible.

Weight loss of piglets due to urination and defaecation was neglected as the piglets urinated and defaecated mainly while they were in the box at weighing before a suckling. The low incidence of urination or defaecation was assumed to be equal for both standardization level piglets. Milk production (not corrected) was 6.00 and 4.24 kg at day 10 and 5.46 and 4.00 kg per day at day 30 of lactation for sows nursing large and small litters respectively. These means were corrected for losses due to metabolic rate and evaporation according to the formula

$$Mc_{ij} = M_{ij} + 24(0.406 + 0.079W_{ij})\ n_j * I_{ij}$$

where Mc_{ij} = average corrected milk production per day (g) at the i-th day (day 10 or 30) and j-th standardization level (high or low)

M_{ij} = average 240 minute milk production (g) times 6.
W_{ij} = average piglet weight (kg)
n_j = number of piglets per litter
I_{ij} = mean interval (minutes) between weighing before and after suckling.

Corrected and uncorrected data per litter and per piglet are given in table 5.1.

Table 5.1 Milk production of sows and milk consumption of piglets at the high and low standardization level.

	day 10		day 30	
	STL_H	STL_L	STL_H	STL_L
Uncorrected milk production per sow (kg/d)	6.00	4.24	5.46	4.00
Corrected milk production per sow (kg/d)	7.89	5.07	8.53	5.52
Uncorrected milk consumption per piglet (kg/d)	0.544	0.729	0.495	0.687
Corrected milk consumption per piglet (kg/d)	0.715	0.870	0.773	0.948
Metabolisable energy of the milk (MJ/kg)*			4.51	4.97
Corrected milk consumption per piglet adjusted for differences in energy value (MJ/d)			3.485	4.710
Creep feed intake (ME) per pig per day from 21 to 35 days (MJ ME/d)**			1.15	1.03

* assuming a ME/GE ratio of 0.92 for sow milk
** assuming 15.5 MJ GE per kg creep feed and a ME/GE ratio of 0.85

Correction for the losses had a larger effect for sows nursing a large than for sows nursing a small litter. This correction affected the difference in milk consumption per piglet between both standardization levels. Without correction this difference was 25 and 30% at days 10 and 30 respectively in favour of piglets raised in small litters. After correction this difference was reduced to 18%.
Sows with a lower milk yield may compensate for reduced energy output by a higher fat content of the milk. So the energy content of the milk produced by sows nursing large compared with small litters might have been lower. Milk samples were not collected in this experiment. Van der Steen (unpublished data) found a decrease in energy content of ca. 9% in milk produced by sows nursing a large litter (12 piglets) over those with a small litter (6 piglets) in the fourth and fifth week of lactation. So milk energy intake was ca. 26% lower for piglets raised in large compared with small litters. By coincidence a similar difference was found in uncorrected milk consumption in g/piglet.
The average milk production per sow per day was 6.5 and 6.9 kg per day at 10 and 30 days after parturition respectively. Klaver et al. (1981) reported the milk production for third parity Dutch Landrace sows of ca. 6 kg at 10 days post parturition. Litters were standardized at 8. Den Hartog et al. (1983) determined milk production in 118 crossbred sows (DL * Y) in which the day of lactation varied from 4 to 33 days. Corrected milk consumption per piglet per day was 677 g. In our experiment the average corrected milk consumption per piglet per day was

321 g. This higher milk consumption may have been due to the lower average litter size (8.4 against 9.2), the stage of lactation (20 against 18 days), breed differences or wrong correction factors.

Creep feed intake per piglet from 21 to 35 days after birth did not differ significantly. It might be argued that the higher milk consumption per piglet at the low standardization level caused the small reduction in creep feed intake. The negative relation between milk consumption and creep feed intake which existed within standardization levels supports this theory. The intake of metabolisable energy from 21 to 35 days of age (milk and creep feed) was ca. 19% lower for gilts raised at the high compared with the low level (table 5.1). This corresponds to the 21% decrease in growth rate from 21 to 35 days of age. Creep feed intake per piglet from weaning to 56 days of age was significantly higher for low standardization level piglets. This was probably due to the higher weight at weaning. As a result of this, growth from weaning to 56 days was higher for low compared with high standardization level gilts.

5.3.2.2 Influences upon growth from birth to weaning

Results given in table 4.12 revealed a clear relation between growth of piglets and milk and creep feed intake. Correction for milk consumption per piglet at day 10, made by including this covariable in the model, resulted in a reduction of 36% in the effect of standardization level on growth from birth to 21 days. Correction for average milk consumption at days 10 and 30 and for creep feed intake resulted in a reduction of 27% in the standardization effect on growth from 21 to 35 days. Relations between intake of milk and creep feed and growth are stronger at the high than at the low standardization level. So milk consumption seems to be a limiting factor for growth especially in large litters. In small litters, variation in growth from 21 to 35 days was mainly associated with the creep feed intake.

In large litters a negative relation existed between the score for stability of the teat order and growth. A stable teat order seems to be favourable for the milk consumption of piglets. Thus a positive relation could be expected. However in large litters more competition between piglets exists as expressed in a lower teat order score. This competition might continue for a longer period in litters with "healthy" piglets. This would explain the negative relation which was found. It was concluded that individual piglets in large litters had a reduced intake of milk, with the effect of strengthening the relation between intake and growth. Barber et al. (1955) stated that the sow's milk production was frequently insufficient to meet the pig's needs for optimum growth. They found that supplementary feed during the last 5 weeks of lactation removed much of the dependence for growth on milk production of the sow. This seemed to be true for small litters but to a smaller extent for large litters.

A lower milk consumption per piglet, lower energy content of the milk and increased competition might explain part of the weight difference at weaning between the two standardization level groups.

Weight gain of piglets was related to milk consumption. Hence a relation between weight gain of piglets and weight loss of the dam from parturition to weaning was to be expected. This weight loss was studied in relation to weight after parturition, milk production and growth of the piglets. Differences in weight loss between sows nursing large and small litters were to a large extent (77%) explained by differences in milk production (tables 4.10 and 4.13). The positive relation between growth of the piglets and weight loss of the dam at a fixed level of milk production and weight after parturition (multiple regression coefficient, table 4.13) suggested that the relation between milk production as measured and realized was not equal to 1. It could also mean that other factors influencing growth of the piglets were determined by the sow.

5.4 Variables measured from 74 days of age to parturition

5.4.1 Growth and backfat thickness during the rearing period

Results given in chapter 4 are summarized in tables 5.2 and 5.3.

Table 5.2 Weight and backfat thickness of both halothane types at the high and low standardization level.

Variable	Halothane negative gilts		Halothane positive gilts	
	STL_H	STL_L	STL_H	STL_L
W74 (kg)	23.2	25.5	22.0	26.6
W186 (kg)	91.1	91.4	83.2	88.5
BFA (mm)	11.94	11.49	9.79	9.68

Table 5.3 Partial regression coefficients of backfat thickness on weight at a constant age at the individual and pen mean level.

	individual data	pen means
$b_{BFA,W186.AW186}$ (mm/kg)	0.128	0.098
$b_{BFA,W186-W74.AW74}$ (mm/kg)	0.150	0.0134

Gilts raised at the low standardization level were heavier at an average age of 74 days than those at the high level. This difference did not exist at 186 days in halothane negative gilts but it remained in halothane positive gilts. Growth per day from 25 to 100 kg in halothane negative gilts was 20 g higher for high than for low standardization level gilts. Growth per day in all gilts was 10 g higher in high standardization level gilts while this difference was 22 g after correction for age at 25 kg. High standardization level gilts deposited more backfat (BFW). The gilts were housed and fed in groups of 4. To calculate the feed conversion ratio (kg feed/kg weight increase) it was necessary to calculate pen means. Pen means were only calculated if data for the four gilts put together at the beginning of the rearing period were available. As a result of this,the data for gilts raised at the low standardization level in two pens of batch 9 were left out of the analysis. It was not possible to correct for halothane susceptibility as both groups were not separately housed. Metabolic weight ($W^{0.75}$) of gilts from batches 9 to 12 were calculated per day and summarized over the period from 74 to 186 days on average (SMW). Results of the analyses are given in table 5.4.

Table 5.4 Influence of standardization level on weight, backfat thickness, feed intake and feed conversion (pen means).

	Batches 9 and 11		Batches 10 and 12		Batches 9 to 12	
y-variable	STL_H	STL_L	STL_H	STL_L	$STL_{(H-L)}$	P_{STL}
model	a				b	
W74	22.3	27.3	23.7	24.2	-2.6	0.09
W186 (kg)	87.8	92.1	90.5	91.2	-2.3	0.23
W186-W74 (kg)	65.5	64.8	66.8	67.0	0.3	0.62
SMW ($kg^{.75}$)	2269	2428	2302	2314	-79	0.21
BFA (mm)	11.71	11.52	11.15	11.46	-0.03	0.99
Feed intake (F.U.)*	209.5	220.5	213.3	213.8	-5.3	0.20
Feed conversion (kg/kg)	3.19	3.40	3.20	3.20	-0.10	0.05
Feed conversion after correction for maintenance requirement	2.04	2.15	2.05	2.04	-0.05	

a model with Batch, STL and Batch by STL interaction effects

b model with Batch and STL effects

* kg creep feed multiplied by 1.03 and sow feed by 0.97 to correct for the difference in energy value between the two types of feed. One feed unit is equivalent to the net energy of 1 kg barley.

Batches 9 and 11 were compared with batches 10 and 12 as the differences in weight at 74 days between the two standardization level groups were large in the former and small in the latter batches. Gilts raised in small as compared with large litters in batches 9 and 11 were 5.0 and 4.3 kg heavier at 74 and 186 days of age respectively. Metabolic weight summarized over the period 74 to 186 days of age was 7% and the feed intake 5% higher. The somewhat lower weight increase and higher feed intake resulted in a feed conversion ratio which was 0.2 higher. Higher weight causes a higher maintenance requirement. This amounts to 420 kJ/$W^{0.75}$ for individually housed pigs (Close and Verstegen, 1981). Adding 10%, as gilts in this experiment were housed in groups of four (Verstegen, personal communications), gives 462 kJ. One feed unit (equivalent to net energy of 1 kg barley) contains

12600 kJ ME. So the maintenance requirement per kg metabolic weight is 0.0333 F.U. Feed intake minus maintenance requirement divided by weight increase for the high and low standardization level gilts of batches 9 and 11 were (209.5 - 2269 x 0.0333)/65.54 = 2.04 and (220.5 - 2428 x 0.0333)/64.84 = 2.15 respectively. Differences in backfat thickness at an age of 186 days were negligible.
It can be conlcuded that:

- compensatory growth of high standardization level gilts was small and the value obscured by the halothane positive gilts.
- backfat thickness of high and low standardization level gilts was the same at 18 days of age in spite of the lower weight of the former. There existed, within standardization level groups, a positive relation between weight and backfat thickness. At a fixed weight (∿100 kg) high standardization level gilts deposite more backfat than low level ones.
- feed conversion ratio was lower in high standardization level gilts in two out of 4 batches, which coincided with a weight difference at 74 days of age. After correction for maintenance requirement this difference was halved. Assuming a higher maintenance requirement would reduce this difference further.

5.4.2 Age at first oestrus

The range in batch means for age at first oestrus was 45 days. The average age was 235 days. In the literature lower values have been reported. Young and King (1981) reported recent experiments in which the average age at first oestrus was between 180 and 200 days. Crossbred gilts were used in these studies. Higher values were also reported. Te Brake (1969) reported a value of 240 days in Dutch Landrace gilts. Differences in age at first oestrus between both standardization level groups were essentially zero which is in agreement with results found by Nelson and Robison (1976b).

5.4.3 Insemination results

The lower conception rate for gilts raised at the high compared with the low standardization level when insemination took place at first oestrus is difficult to explain. As the opposite result was obtained when insemination took place at second or later oestrus the average conception rate was equal for both groups. At the high standardization level 20 percent of the gilts which produced a litter did so as a result of insemination at the first oestrus while at the low level this percentage was 49. This result was obtained although the age at first oestrus and conception rate were not affected by the standardization level and gilts were inseminated at a fixed age.

5.5 Influence of standardization level on litter size

Oestrus number at insemination and halothane susceptibility affect litter size. There are two ways to eliminate the effect of halothane susceptibility by either including the factor in the model or using the data of halothane negative gilts only. Data of batches 6 to 12 (halothane susceptibility was tested) or data from batches 9 to 12 (high and low standardization level gilts) were used. The results are summarized in table 5.5.

Table 5.5 Influence of standardization level on the size of the first litter.

	halothane negative gilts only	all gilts; HAL-effect in the model	halothane negative gilts only	all gilts; HAL-effect in the model
$TL_{(H-L)}$	-0.48	-0.32	-0.62	-0.57
m-value	-0.089	-0.059	-0.115	-0.106

From a total of 111 high and low standardization level gilts which produced a litter, 96 were halothane negative. As the frequency of halothane positive pigs is decreasing in the Dutch Landrace population, as a result of selection against the halothane positive gene (Eikelenboom, 1980), the estimate of standardization level effect obtained in halothane negative gilts seems to be the most appropriate one. Using data from batches 6 to 12 gives the most accurate correction for oestrus number at insemination. The resulting value of -0.48 gives an estimate of the m-value defined by Falconer (1965) of -0.09 (-0.48/5.4) as the realized difference in standardization level was 5.4 piglets.

Uterus weight of low compared with high standardization level sows was higher. They also tended to have longer uterus horns. This was not caused by the direct effect of a larger first litter as the uncorrected means did not differ. Being raised in small litters might have a positive influence on the development of the uterus.

A tendency for a higher number of corpora lutea in low compared with high standardization level gilts was observed in sows in which oestrus was induced. Robison (1979) suggested that a high litter size during the suckling period would have a negative influence on weaning weight, development of the gilts, age at first oestrus and hence oestrus number at insemination. This would result in a lower litter size of the gilt raised in a large litter. Litter size during the suckling period influence the weaning weight but no influence upon age at first oestrus and weight at insemination was observed. The oestrus number at insemination was even higher for gilts raised in large litters although the age at first oestrus and conception rate were not affected by the standardization level and gilts were inseminated at a fixed age.

Of the determinants of litter size, ovulation rate and embryo survival, only the first differed in Nelson and Robison's material. Rutledge (1980) concluded: "The mechanism may involve the neonatal ovary. Oogenesis in the pig begins before day 40 of fetal life (Black and Erickson, 1968) and lasts until at least day 35 post-partum (Fulka et al., 1972). Degeneration is common during this period, with only an estimated 50% of the germ cell population surviving transformation in the pig (Black and Erickson, 1968). Oocytes surviving transformation and entering meiotic arrest are enveloped by a few granulose cells. This unit, the primordial follicle, comprises the majority of follicles in the mature ovary. A small fraternity size might provide conditions avoiding degeneration and results in a larger pool of primordial follicles. If the pool were larger, increased ovulation rate and litter size could be predicted not only for first, but also for subsequent parities".

The influence of standardization level on the number of corpora lutea after induction of oestrus after weaning of the first litter is, in our experiment, in line with the hypothesis postulated by Rutledge (1980). Cunningham et al. (1979) found no correlated response in litter size after successful selection for ovulation rate. Thus, a higher ovulation rate does not necessarily result in increased litter size. Results obtained suggest that a low standardization level affects weaning weight and development of the uterus positively. This, in combination with a larger pool of primordial follicles, might explain the positive effect on litter size.

5.6 Implications of the maternal influence for selection on litter size

5.6.1 Theory

Pre- and post-natal maternal influences were defined in appendix 9. The maternal effect as defined by the size of the litter can be separated into two components determined by the size of the litter during pregnancy (P'_b) and size of the litter during the suckling period (P'_s) respectively.

If $P'_b = P'_s$ we can write

$$P_x = m_1P'_b + m_2P'_s = (m_1 + m_2)\ P' = m\ P'$$

The average value for estimates of m_2 in mice were equal to -0.07 (section 2.4). The result obtained in pigs by Nelson and Robison (1976b) (m_2 = -0.11) was more in agreement with the result obtained in this experiment (m_2 = -0.09) than the estimate calculated from results reported by Rutledge (1980) (m_2 = -0.20). A value for m_2 of -0.20 seems unlikely as this affects the daughter-dam regression coefficient to such an extent that positive heritability estimates by daughter-dam regression could not be expected. So the parametric value of m_2 seems to be somewhere between -0.075 and -0.125. As the few estimates of (m_1 + m_2) suggest a value of $\sim$-0.125 (table 2.5), m_1 seems to be 0 to -0.05.

A general formula for the regression of daughters' first litter size on dams' first litter (birth litter) can be derived from formula 15 of appendix 9.

$$b_{PP'} = \frac{V_A}{V_{P'_b}} \left(\frac{1}{2-m_1-m_2}\right) + m_1 + m_2\, r\, (V_{P'_s} / V_{P'_b})^{\frac{1}{2}} \qquad (12)$$

If litters are not standardized then $V_{P'_b} \cong V_{P'_s}$
and $r \cong 1$, so

$$b_{PP'} = \frac{V_A}{V_{P'}} \left\{ \frac{1}{2-(m_1+m_2)} \right\} + (m_1 + m_2) \qquad (13)$$

Standardization of litters given $V_{P'_s} = 0$ and

$$b_{PP'} = \frac{V_A}{V_{P'}} \left\{ \frac{1}{2-m_1} \right\} + m_1 \qquad (14)$$

Granddaughter - granddam regression coefficients in similar circumstances are

$$b_{PP''} = \frac{V_A}{V_{P''}} \left\{ \frac{\frac{1}{2}+(m_1+m_2)}{2-(m_1+m_2)} \right\} + (m_1 + m_2)^2 \qquad (15)$$

and

$$b_{PP''} = \frac{V_A}{V_{P''}} \left\{ \frac{\frac{1}{2}+m_1}{2-m_1} \right\} + m_1^2 \qquad (16)$$

These regression coefficients were calculated and results are given in table 5.6.
ssumed parameters were:

$_A$ = 1.25; $V_{P''}$ = 6.25 so h^{2*} = 0.2

$_1$ = 0 or -0.05; m_2 = -0.075, -0.100 or -0.125.

Table 5.6 Effect of standardization of litters on daughter-dam and granddaughter-granddam regression coefficients.

litters standardized:		daughter-dam regression		granddaughter-granddam regression	
m_1	m_2	no	yes	no	yes
0	-0.075	0.021	0.100	0.047	0.050
	-0.100	-0.005	0.100	0.048	0.050
	-0.125	-0.031	0.100	0.051	0.050
-0.05	-0.075	-0.031	0.048	0.051	0.046
	-0.100	-0.057	0.048	0.055	0.046
	-0.125	-0.083	0.048	0.061	0.046

Daughter-dam regression coefficients are seriously biased by pre- and post-natal maternal effects while granddaughter-granddam estimates are biased to a much smaller extent using this range of parameter values.

5.6.2 Simulation study

5.6.2.1 The procedure

A Monte Carlo simulation study was carried out to examine the effect of pre- and post-natal maternal influences upon daughter-dam and granddaughter-granddam regression coefficients. Situations with and without selection for litter size and several standardization strategies were included. First litter data were simulated. The following model was used.

$$P_{ijk} = \mu + \tfrac{1}{2} A_i + \tfrac{1}{2} A_j + \sqrt{\tfrac{1}{2}}\; r_1 V_A^{\frac{1}{2}} + m_1 P'_b + m_2 P'_s + r_2 V_E^{\frac{1}{2}} \tag{17}$$

where P_{ijk} = litter size of k-th daughter of j-th dam and i-th sire.
μ = 9 piglets
A_i = additive genetic value of i-th sire
A_j = additive genetic value of j-th dam
V_A = additive genetic variance component
V_E = environmental variance component
$m_1 P'_b$ = pre-natal maternal effect
P'_b = litter size at birth of the dam
$m_2 P'_s$ = post-natal maternal effect
P'_s = size of the litter of the dam during the suckling period (standardization level)
r_1, r_2 = normal deviates; N (0,1).

The value of P's depended upon the standardization procedure. The alternatives were

1. Litters were not standardized (P's = P')
2. Litters were standardized at the population mean of generation 0 (P's = 9)
3. Large and small litters were standardized (P'≤ 9-C_1 then P's = 9-C_1; P'≥ 9+C_2 then P's = 9+C_2)
4. Litters were standardized at a fixed level (P's = 9+C_3)

C_1, C_2 and C_3 were terms that could be varied.

A variable number of generations and a variable number of replicates could be simulated. $V_A + V_E$ was set at a fixed value of 6.25; being the phenotypic variance of litter size. $V_A/(V_A+V_E)$ was 0.1 or 0.2.

Values for m_1 and m_2 were 0 or -0.05 and 0, -0.075, -0.100, -0.125 or -0.200 respectively. The genetic structure at each generation was hierarchical i.e. 20 sires, 5 dams per sire and 4 daughters per dam. So 400 first litters were simulated at each generation for each replicate.

A linear relation between the post-natal maternal effect on litter size and P's was assumed. Data for pigs are not available to test this assumption. However a linear relation between the post-natal maternal effect on weaning weight and weight just before breeding seems to exist in mice as illustrated in figures 5.3 and 5.4. Consequently the assumption that a similar relation exists in pigs may not be unjustified.

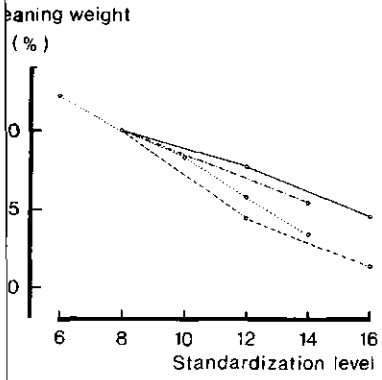


Fig. 5.3 Influence of standardization level on weaning weight in mice. Weight at a standardization level of 8 was set at 100%.

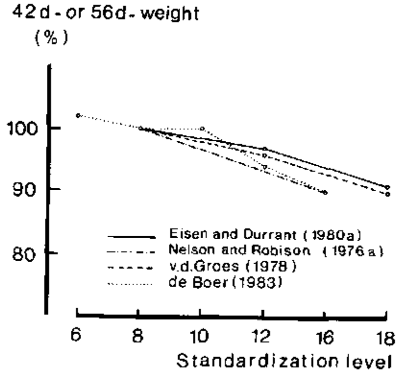


Fig. 5.4 Influence of standardization level on 42 d- or 56 d-weight in mice. Weight at a standardization level of 8 was set at 100%.

5.6.2.2 Effect of pre- and/or post-natal maternal influence upon daughter-dam and granddaughter-granddam regression coefficients.

For each combination of m_1 with m_2 data of 11 generations were simulated. This was repeated 10 times. As can be seen from equations 13 and 15, the value of $m_1 + m_2$ is relevant. The regression coefficients which were calculated are given in figure 5.5.

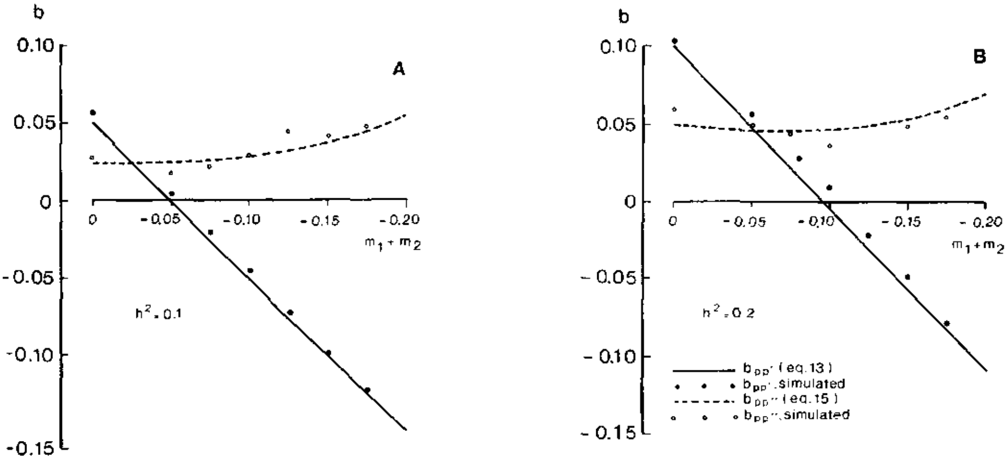


Fig. 5.5 The maternal effect on daughter-dam and granddaughter-granddam regression coefficients.

Each value of a daughter-dam regression coefficient is the average of 100 regressi coefficients (10 pairs of generations, 10 replicates). Individual regression coefficients are based on 400 daughter-dam pairs. A granddaughter-granddam regression coefficient is the average of 90 individual regression coefficients. Th expected values, according to equations 13 and 15 are equal to the values calculat from simulated data. Daughter-dam regression coefficients were increasingly biased as the value of $m_1 + m_2$ became more negative. Granddaughter-granddam regression coefficients were biased upwards by large negative values of $m_1 + m_2$ especially when heritability for litter size was low. The standard deviations of the individual daughter-dam and granddaughter-granddam regression coefficients were ca 0.055 and 0.058 respectively.

Standardization of litters will eliminate the post-natal maternal effect, as defined by the model (eq. 17). Standardization to some extent by standardizing litters smaller than 9-C at 9-C and litters larger than 9+C at 9+C removes part of the post-maternal influence. This is illustrated by figure 5.6.

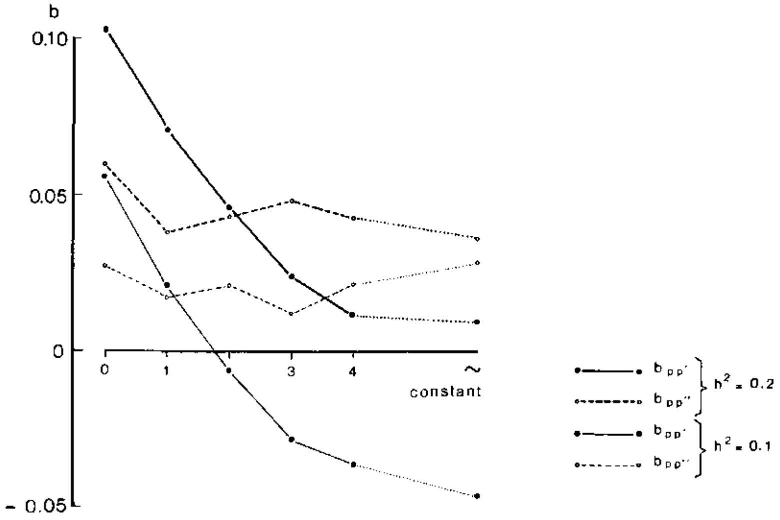


Fig. 5.6 Influence of standardization of litters on daughter-dam and granddaughter-granddam regression coefficients. Litters ≥9+C standardized at 9+C and litters ≤9-C standardized at 9-C piglets.

Even a small deviation from standardizing all litters at 9 results in a substantial reduction in the daughter-dam regression coefficient.

5.6.2.3 Effect of pre- and/or post-natal maternal influence on response to selection

Maternal influences affect the response to selection in two ways. Firstly the relation between additive genetic value and phenotypic value will be changed.

$$b_{A,P} = \frac{\text{cov }(A,P)}{\sigma^2_P}$$

where

$$\begin{aligned}\text{cov }(A,P) &= \text{cov }(A,\ A + M_1 + M_2 + R)\\ &= V_A + \text{cov }(A,M_1) + \text{cov }(A,M_2)\\ &= V_A\ (1 + \frac{m_1+m_2}{2-m_1-m_2})\end{aligned}$$

so

$$b_{A,P} = h^2 * \ (1 + \frac{m_1+m_2}{2-m_1-m_2}) \qquad (18)$$

The coefficient $(1 + \frac{m_1+m_2}{2-m_1-m_2})$, for $m_1 + m_2 = -0.1$ or -0.2 equals 0.95 and 0.89 respectively. This causes a small reduction of the selection response. Secondly, maternal effects result in a permanent negative effect on litter size as, in a selection programme for litter size, the next generation of gilts will be born and raised in large litters.

Simulation results are given in figures 5.7.

Progeny were selected from first litters only. Gilts were selected from the larges litters (p_D = 0.25 or 0.50), boars were selected from the largest litters (p_S = 0.25) or gilts and boars were selected from the largest litters ($P_D = p_S$ = 0.25). The response to selection of boars from the largest litters is affected by materna influences due to the reduced regression coefficient of additive genetic to phenotypic value only (figure 5.7 B and D). This reduction agrees with that predicted by equation 18. Selection of gilts from the largest litters results in a permanent maternal effect and a reduced rate of response (figure 5.7 A and C). The extent of this permanent maternal effect on litter size depends on the value of $m_1 + m_2$, the intensity of selection and the phenotypic standard deviation ($m\ i\ \sigma_P$).

The number of generations of selection (k) needed to overcome this reduction depends on the heritability, the value of $m_1 + m_2$ (= m) and the intensity of selection of gilts and boars if these (i_D and i_S) are not equal.

permanent maternal effect = $(m_1 + m_2)\ i_D\ \sigma_P$

response to selection of gilts and boars = $(\frac{1}{2}\ b_{AP}\ i\ \sigma_P)\ k$, if $i_D = i_S$

$$\text{so } \tfrac{1}{2}\ h^{2*}\ (1 + \frac{m}{2-m})\ i\ \ \sigma_P\ k + m\ i\ \sigma_P = 0$$

$$\text{thus } k = (m^2 - 2m)\ /\ h^{2*}$$

It takes 4.4 or 2.2 generations of selection to overcome the initial negative response to selection for litter size if $m_1 + m_2 = -0.2$ at $h^2 = 0.1$ and 0.2 respectively. The negative effect of post-natal maternal influences on the selection response will be reduced if litters are standardized. This is illustrated in figure 5.8.

The variability of the response to selection is illustrated by figure 5.9. A selection intensity of 25% results in a phenotypic difference of ca. 3.2 piglets which causes the permanent negative effect on litter size, although the breeding value of the mothers is positive.

The reduction of the regression coefficient of additive genetic to phenotypic valu by maternal effects can be eliminated by correction of the data. For this purpose accurate estimates of m_1 and m_2 are needed. It is doubtful whether this correction is worthwhile as the effects on the regression coefficient are small.

Pre- and post-natal maternal effects cause an important permanent reduction in litter size if selected gilts are born and raised in large litters. Post-natal

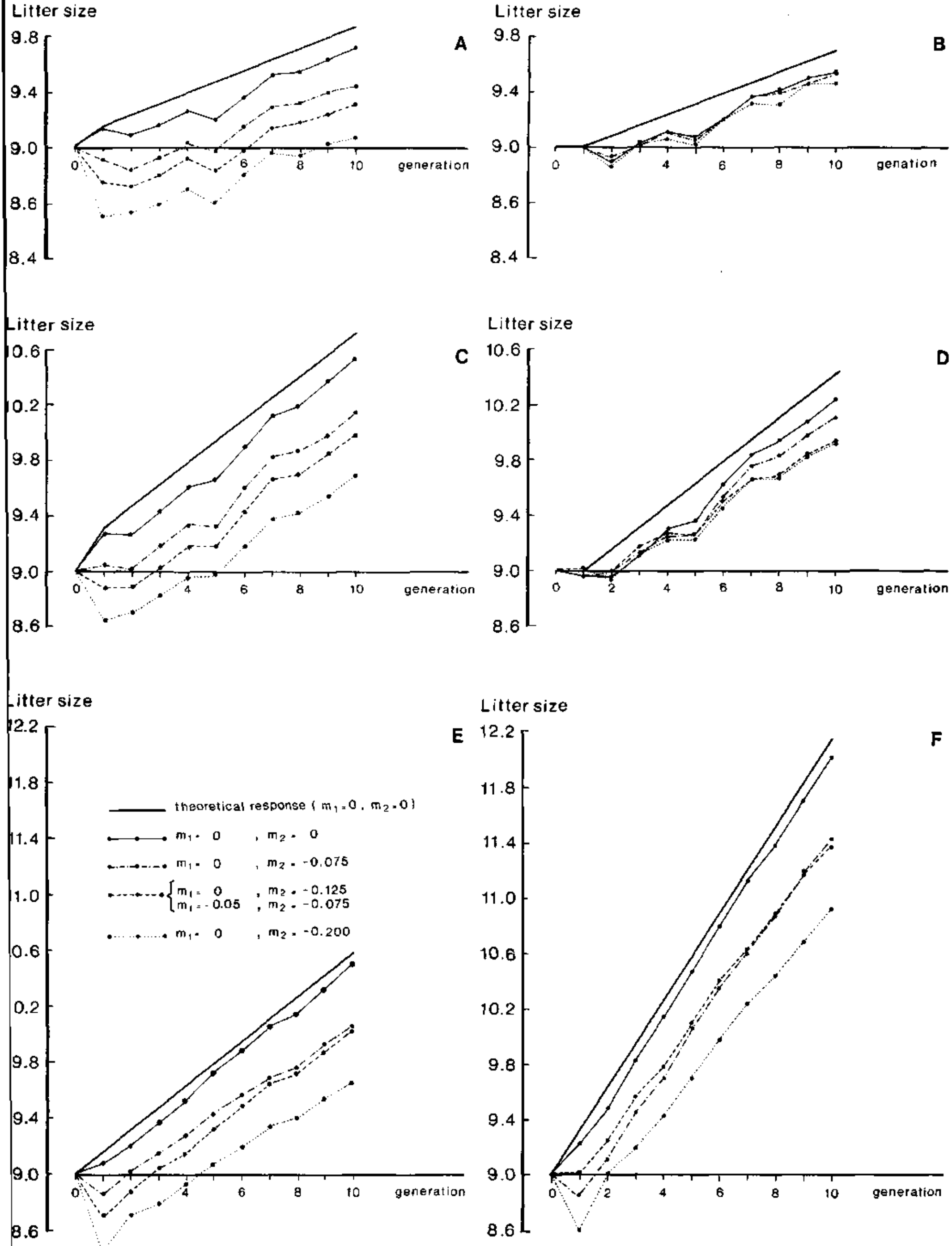


Fig. 5.7 The maternal effect on response to selection for litter size. A. $h^2=0.1$, gilts selected, $p_D=0.25$; B. $h^2=0.1$, boars selected, $p_S=0.25$; C. $h^2=0.2$, gilts selected, $p_D=0.25$; D. $h^2=0.2$, boars selected, $p_S=0.25$; E. $h^2=0.1$, gilts and boars selected, $p_D=p_S=0.25$; F. $h^2=0.2$, gilts and boars selected; $p_D=p_S=0.25$.

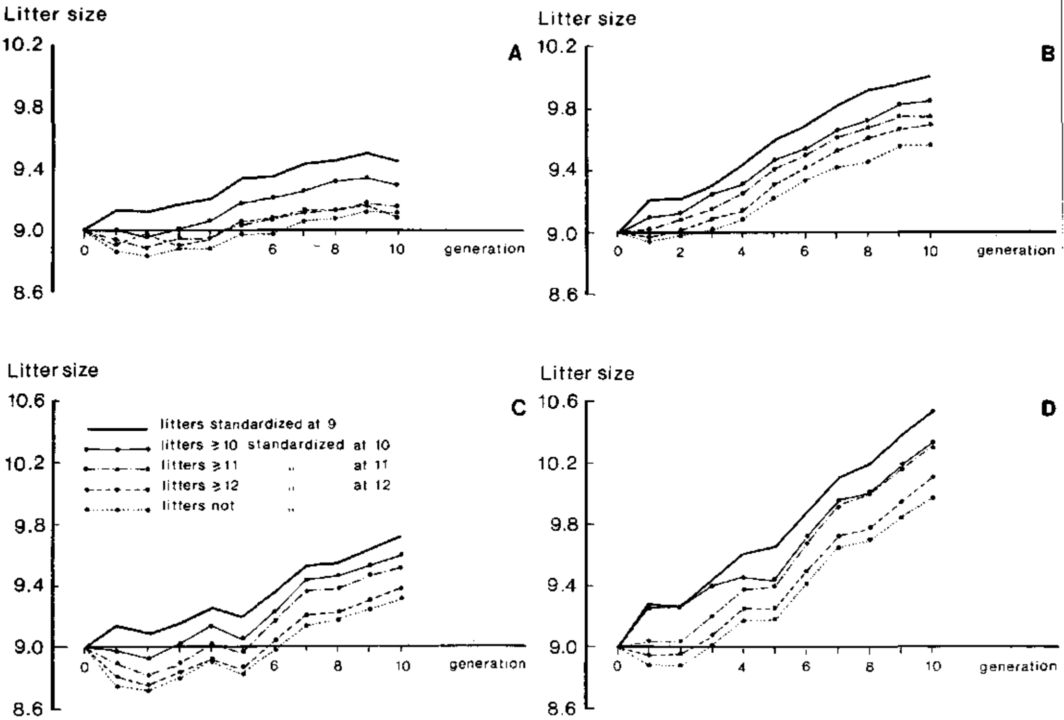


Fig. 5.8 The effect of standardization of litters on response to selection for litter size (m_1=0, m_2=−0.125). A. h^2=0.1, gilts selected, p_D=0.50; B. h^2=0.2, gilts selected, p_D=0.50; C. h^2=0.1, gilts selected, p_D=0.25; D. h^2=0.2, gilts selected, p_D=0.25.

effects can eliminated by standardization of litters at the population mean.

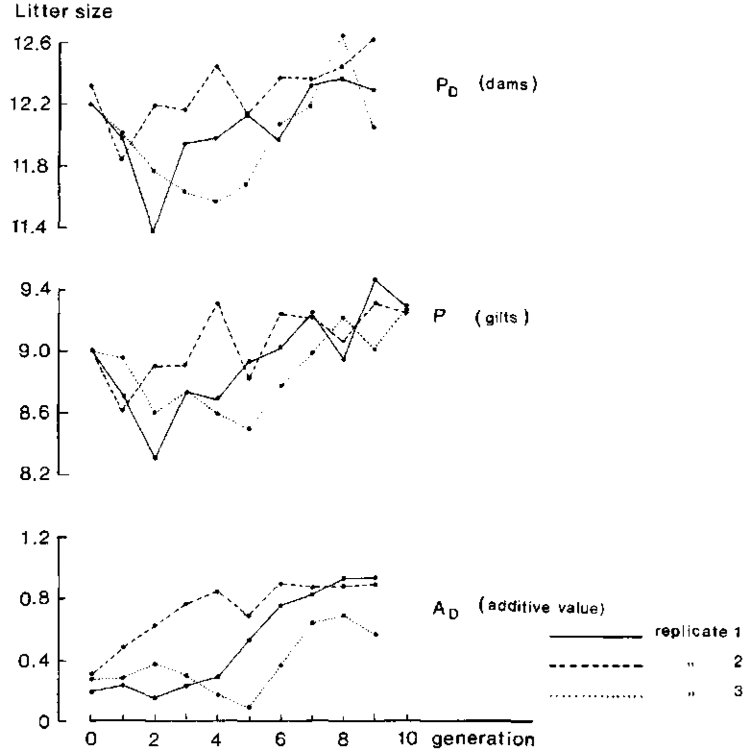


Fig. 5.9 The maternal effect on litter size of all gilts (P) and additive genetic (A_D) and phenotypic value (P_D) of gilts which will produce the next generation (gilts selected, p_D=0.25;h^2=0.1; m_1=0; m_2=-0.125; three replicates).

Maternal effects reduce the increase of additive genetic value due to selection for litter size to a small extent. Rutledge (1980) states: "Over a range of plausible values for the parameters of the model, the daughter-dam correlation for numbers born tended to be negative. Thus, selection of replacement gilts born and reared in large litters would not bring about desirable genetic changes in litter size". Our interpretation of the results does not agree with this conclusion as the regression coefficient of additive to phenotypic value is applicable.Over a range of plausible values for m_1 + m_2 this regression coefficient and thus genetic change decreased by 5 to 10% due to maternal effects.

So the genetic implications of maternal effects on litter size are limited. Selection will result in an additive genetic response. The practical implications are important. The permanent negative environmental effect on litter size, if replacement gilts are born and raised in large litters, does reduce the phenotypic value. To a large extent, standardization of litters will remove this,from an economic point of view, unfavourable effect. The response to several generations of selection for litter size might be zero because of this permanent negative environmental effect and/or the limited size of the experiment. Selection for fertility is possible but is not always evident because too few animals have been used. Large scale experiments are needed to improve litter size or overall reproductive performance by selection. Overall reproductive performance involves the age at first oestrus, litter sizes at birth and weaning at different parities, birth weights and weaning weights, interval from weaning to oestrus and conception rate.

Points of interest for the future are

- assessing the economically important components of overall reproductive performance
- achieving accurate estimates of genetic and phenotypic correlations and heritabilities involved and
- combining the sources of information in an index. This index will combine several traits measured on the individual and/or relatives. An economic evaluation of selection strategies is needed.

5.7 The influence of halothane susceptibility

Differences between halothane negative and positive gilts are summarized in table 5.7.

Table 5.7 Differences between halothane negative and positive gilts.

Trait	halothane negative	halothane positive
Weight (kg)		
W74	25.2	24.6
W214	106.6	102.1
WEI	131.1	127.7
WBP	195.4	190.5
WAP	177.1	174.6
BFW (mm)	12.29	11.24
AFOMS (d)	242.1	243.0
Conception rate (%)	70	75
NPT	10.04	8.77
WU (g)	599	496
LUH (cm)	291	250

Differences in growth were small which agrees with the conclusions of Eikelenboom (1981) and Webb et al. (1982). A lower backfat thickness at a fixed weight of approximately 100 kg in reactors was reported in the literature. A difference of 1 mm was also calculated from the results of 14 studies by Webb et al. (1982).

The influence of halothane susceptibility on reproduction traits is of particular interest as results of only one study have been reported (Webb, 1982). Differences in age at first oestrus and conception rate were not significant. Webb (1982) reported a reduction in conception rate of halothane positive gilts while in our experiment the small difference was in favour of the halothane positive gilts. The reduction in litter size (-1.3) was in close agreement with the value reported by Webb (1982). As the number of corpora lutea after weaning of the first litter did not differ significantly between both halothane types it might be speculated that embryonic and foetal mortality is higher in halothane positive gilts. This might be due to a higher % of halothane susceptibility in the litter and poorer uterine capacity, as uterus weight and length of the uterus horns was significantly reduced in halothane positive sows.

5.8 Differences between batches

Differences between batches were significant for almost all variables measured or calculated. Batch differences may be caused by year-, season- or other effects. Differences between years may be due to genetic differences, environmental changes, such as level of infection, and/or disease resistance, unintended changes of management etc. These factors cannot be separated.

Differences between the four periods can be considered as season effects. The period effect on growth is summarized in appendix 4. The period number reflects the period of birth. There were no birth periods which resulted in a higher growth rate from birth to 56 days of age, from 74 to 214 days, or from insemination to parturition. Average growth per period as a percentage of the mean, in relation to the season (month) when growth actually took place, is given in figure 5.10. Pigs grew relatively slowly from February to May and fast from August to November. A similar result was found by Ketelaars (1979).

Backfat thickness was greatest in birth periods 1 and 4. Growth during the rearing period (W214-W74) was also highest in those periods. So relatively fast growth during the rearing period coincided with more backfat at the end of this period. A positive correlation between those variables was also found within batches. More metabolisable energy is required for fat deposition than for an equal weight of lean tissue. The variation in backfat thickness between periods and within batches may be caused by various factors. These include differences in digestibility, efficiency of energy retention, or maintenance requirement. It is also possible that backfat thickness is not an optimal indicator of the total fat content of the body.

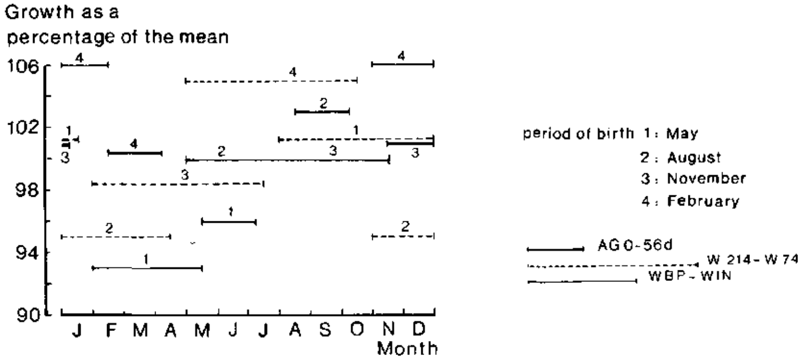


Fig. 5.10 Seasonal influence on growth.

The negative relation of backfat thickness to weight before parturition between batch means (figures 8 E and F) was caused by differences between generations (figures 4.4 and 4.5; appendix 4). Gilts of generation three had less backfat (1.1 mm at ∿100 kg) and were heavier at parturition (11 kg) than those of generation one. This was caused by a greater weight increase from the age of 186 days to parturition (figure 4.7). Environmental or genetic differences might have caused this. Gilts of generation one were purchased from multiplier herds. Of those gilts 26% descended from A.I. boars while all gilts of generation two and three descended from A.I.-boars. Those boars represent the nucleus of the Dutch Landrace population. Genetic differences between the three generations probably exist as the genetic time lag, as defined by Bichard (1971) between multiplier herds and nucleus, will be substantial.

The year effect on weight before parturition also caused the negative relation between batch means of weight at 56 days to weight before parturition (figure 8 C). The year effect on weight at 56 days was relatively small (the axes in figure 8 represent three times the standard deviation of the trait). Correlation coefficient within batches are determined by the heritabilities of and genetic correlations between traits, (micro) environmental variation and genotype-environmental interaction. Factors as disease (resistance), environmental differences between pens, competition between gilts within a pen etc. may be of importance. Correlation coefficients between batches will determined by genetic and environmental trends, seasonal variation and factors with no systematic pattern, such as the occurence of (sub-clinical) diseases. Correlation coefficients between batches are changeable and may affect the overall correlation coefficients.

Figures 8 A and B demonstrate the differences within and between batches in correlation coefficients of backfat thickness and weight at 186 days with age at first oestrus. Within batches this relation is weak while it is strong and negative between batches.

A higher weight and more backfat coincided with a lower age at first oestrus. A favourable environment for growth may also reduce age at first oestrus. Hutchens et al. (1981) reported phenotypic correlation coefficients of age at puberty with backfat thickness (0.01) and post-weaning daily gain (-0.34).
A seasonal effect on age at first oestrus was detected. Gilts of period 1 and 4 came on heat for the first time at a relatively low age. Those gilts showed first oestrus in December/January and September/October respectively. Age at first oestrus was highest in June/July. Seasonal influences on age at first oestrus are scarcely documented in the literature.
Seasonal effects were sometimes included in the model but estimates were not reported (e.g. Hutchens et al., 1981) or age at first oestrus was not recorded (e.g. Hurtgen et al., 1980). A poor level of post-weaning fertility from July through September was reported by Hurtgen et al. (1980). Ricordeau (1982) concluded from a literature review that reproductive efficiency decreased during the summer months (minimum in June, July, August). This seasonal infertility included delayed puberty. Seasonal effects may depend upon type of housing, feeding and climate.

SUMMARY

The profitability of pig production may be expressed as a function of reproductivity and productivity. The optimal selection pressure on reproductivity relative to productivity depends on the response to selection and the economic value of the response. Reproductive performance is primarily a function of the dam and involves age at first oestrus, conception rate, litter size and the interval between weaning and oestrus. An increase in the litter size would improve the reproductive performance. Mean litter size has been rather constant in most countries over the last decades. This means that there has been no response to selection or no selection pressure on litter size. It could also imply a relatively deterioration in the environment or negative effects of selection for production characteristics. It has not been established whether selection for litter size is worthwhile. The heritability of the trait, possible selection differential and the economic value of litter size are important components determining the response to selection. Of these, heritability seems to be the major limiting factor. Estimates of this factor have been consistently low ($\sim$0.10). A negative correlation between direct genetic and maternal effect might reduce the effective heritability or response to selection. A dam may influence her offspring through the environment she provides as well as through the genes transmitted to the offspring. This environmental effect of the dam on her offspring is referred to as maternal influence. The present study was focussed on the effect of the post-natal maternal conditions on the fertility of the daughter.
Maternal influences are partly due to the size of the litter in which a gilt is raised. Gilts raised in small compared with large litters might produce larger litters. This maternal influence affects h^2 estimated by daughter-dam regression but not h^2 estimated by paternal half sib analysis.
It is not clear how important the maternal influence on litter size is. Systematic differences in h^2 estimated by daughter-dam or paternal half sib analysis, have not been found. A negative effect of being raised in large litters on the size of the first litter from gilts raised in large litters was reported (table 2.6). So maternal effects might counterbalance the response to selection for litter size

The experiments were performed to estimate the effect of standardization level (litter size during the suckling period) on the development of the gilt, age at

puberty, size of the first litter and number of corpora lutea after first oestrus of the weaned primiparous sow. The effect of maternal influences on the response to selection was studied by simulation.

Three generations of Dutch Landrace gilts were reared. The first generation (192 gilts) was purchased and the litters produced were standardized at 8 piglets within 24 hours of birth. Litters produced by the gilts of generation two were standardized at 6 (low level) or 12 piglets (high level). Thus the effect of the standardization level on production and reproduction traits was measured in gilts of generation three. Gilts were inseminated at a fixed age of approximately 255 days.

Growth of litters from birth to weaning at five weeks of age, expressed per piglet, at the high standardization level was 24% lower than those at the low level. From weaning to 56 days of age the difference was 8%. This resulted in a weight at 56 days of 15.8 and 18.7 kg for gilts raised at the high and low levels respectively. Milk energy intake was ca. 26% lower for piglets raised in large compared with small litters. The intake of milk and creep feed (ME) from 21 days to weaning was reduced by ca. 19% (table 5.1). Relations between intake of milk and creep feed, and growth were stronger at the high than at the low standardization level. Milk production is a limiting factor for growth especially in large litters.

The significant weight difference between both standardization level groups at 56 and 74 days of age had disappeared at insemination. At a fixed weight (∿100 kg) high standardization level gilts deposited more backfat than those standardized at the low level.

At the high standardization level 20% of the gilts that produced a litter did so as a result of insemination at the first oestrus while at the low level this percentage was 49. This result was obtained although the age at first oestrus and conception rate were not affected by the standardization level, and gilts were inseminated at a fixed age.

From a total of 111 high and low standardization level gilts which produced a litter, 96 were halothane negative. The estimate of standardization level effect on litter size obtained from halothane negative gilts, after correction for oestrus number at insemination, was -0.48 piglets (high-low; table 5.5). The realized difference in standardization level was 5.4 piglets which resulted in an estimate of the "m-value", defined by Falconer (1965), of -0.09. The coefficient m is the partial regression coefficient of daughters' phenotypic value on mothers' phenotypic value for litter size in the absence of genetic variation among the mothers. This m value can be split into a pre- and a post-natal component m_1 and m_2 ($m = m_1 + m_2$). Uterus weight was higher in low compared with high standardization level sows. The former also tended to have longer uterus horns. A tendency to a higher number of corpora lutea in low than in high standardization level gilts was observed in sows in which oestrus after weaning of the first litter was induced. Results obtained suggest that a low standardization level positively affects weani weight and development of the uterus. This, in combination with a larger pool of primordial follicles might explain the positive effect on litter size.

From a simulation study and derived formulae it was concluded that daughter-dam regression coefficients (trait: first litter size) are seriously biased by pre-and post-natal maternal effects while granddaughter-granddam estimates are biased to a much smaller extent (fig. 5.5). Standardization of litters will eliminate the post-natal maternal effect as determined by litter size during the suckling period
Maternal influences affect the response to selection in two ways. Firstly the relation between additive genetic value and phenotypic value will be changed. A value of -0.1 or -0.2 for m reduced the regression coefficient by 5 and 11% respectively. Secondly, maternal effects result in an important permanent negative effec on litter size as, in a selection programme for litter size, the next generation of gilts will be born and raised in large litters. Selection of boars only from the largest litters does not result in a permanent negative effect.
The reduction of the regression coefficient of additive genetic value to phenotypi value by maternal effects can be eliminated by correction of the data. For this purpose accurate estimates of m_1 and m_2 are needed. It is doubtful whether this correction is worthwhile as the effect on the regression coefficient and thus on the response to selection is small. Standardization of litters will be more efficient as it also removes the permanent negative effect on litter size as far as is determined by post-natal maternal effects.
It cannot be concluded from a negative daughter-dam correlation for number born that selection of replacement gilts born and raised in large litters would not bring about desirable genetic changes in litter size. The value of the regression coefficient of additive to phenotypic value is of significance. Over a range of plausible values for m this regression coefficient, and thus genetic change, decreased by 5 to 10% due to maternal effects.
So the genetic implications of maternal effects on litter size are limited. Selection will result in an additive genetic response. The permanent negative environmental effect on litter size, if replacement gilts are born and raised in large litters, does reduce the phenotypic value. To a large extent, standardizatio of litters will remove this, from an economic point of view, unfavourable effect. The response to several generations of selection for litter size might be zero

because of this permanent negative environmental effect and/or the limited size of the experiment. Selection for fertility is possible but is not always evident because too few animals have been used. Large scale experiments or lines in which litters are standardized are needed to improve litter size or overall reproductive performance by selection. Points of interest for the future are

- assessing the economically important components of overall reproductive performance
- achieving accurate estimates of genetic and phenotypic correlations and heritabilities involved
- combining the sources of information in an index and
- assessing an optimal selection scheme.

It may be postulated that the rather constant mean litter size over the last decades is probably caused by a low realized selection pressure. A higher selection pressure in combination with more efficient methods (larger scale experiments, standardization of litters, accurate data collection, combining sources of information) practized over a period of 10 years or more will result in a response to selection which is of economic interest.

SAMENVATTING

Het rendement van de produktie van varkensvlees kan worden uitgedrukt als een functie van produktie- en reproduktiekenmerken. Door middel van een gerichte selectie is het mogelijk om dit rendement te verhogen. De optimale verhouding tussen selectie op produktie- en reproduktiekenmerken is afhankelijk van de te verwachten selectierespons per kenmerk en de economische waarden daarvan. De vruchtbaarheidskenmerken worden hoofdzakelijk bepaald door de zeug. Belangrijke componenten van de vruchtbaarheid zijn: leeftijd bij eerste bronst, drachtigheidspercentage, toomgrootte en het interval spenen-bronst. Het kengetal "aantal biggen per zeug per jaar" combineert deze componenten met de lengte van de dracht en de zoogperiode. Vooral een afname van de lengte van de zoogperiode heeft geleid tot een toename van het kengetal. De toomgrootte is gedurende de laatste decennia in de meeste landen niet toegenomen. Dit kan worden toegeschreven aan het ontbreken van een selectiedruk of het ontbreken van een respons op selectie. Ook kan het zijn veroorzaakt door een relatief verslechterend milieu (voeding, huisvesting, gezondheid) of negatieve effecten van selectie op produktiekenmerken.

De mogelijkheden van selectie op worpgrootte bij varkens zijn nog niet aangetoond door middel van succesvolle selectie-experimenten. Het rendement van selectie op worpgrootte wordt in belangrijke mate bepaald door het aan te leggen selectieverschil, de erfelijkheidsgraad en de economische waarde van het kenmerk. Hiervan is de erfelijkheidsgraad de meest beperkende factor. Schattingen van de erfelijkheidsgraad leverden een gemiddelde waarde op van ca. 0,10.

Een moeder kan haar nakomeling beïnvloeden zowel door de genen die worden doorgegeven als door het milieu dat ze vormt voor haar nakomelingen. Dit door de moeder bepaalde milieu-effect op de nakomeling wordt aangeduid als het maternale effect. Maternale invloeden kunnen worden opgesplitst in pre- en post-natale maternale invloeden. Vóór de partus spelen factoren als cytoplasmatische effecten, baarmoedercapaciteit en aantal foeten een rol. Na de partus betreft het o.a. melkproduktie, moederzorg en toomgrootte. De lage h^2 en daarmee de beperkte selectierespons zou verklaard kunnen worden door een negatieve correlatie tussen de additief genetische waarde van en het maternale effect op worpgrootte.

Het onderhavige onderzoek was gericht op het effect van de post-natale maternale invloed op de vruchtbaarheid van de dochter. Dit post-natale maternale effect wordt voor een deel bepaald door de grootte van de toom waarin een gelt opgroeit. De grootte van de toom wordt voor een belangrijk deel bepaald door de moeder. Gelten die moeten opgroeien in grote tomen zouden ondanks een gunstige genetische aanleg daardoor kleinere tomen kunnen produceren. Deze maternale invloed verlaagt de h^2 geschat met behulp van dochter-moeder regressie. De schattingen met behulp van paternale half-sib analyse worden niet verstoord door maternale invloeden.

Op grond van de literatuur kan geconcludeerd worden dat er geen systematische verschillen bestaan tussen h^2-ten geschat met behulp van dochter-moeder regressie en paternale half-sib analyse. Nelson en Robison (1976b) daarentegen vonden een negatieve invloed van het opgroeien in grote tomen (14 t.o.v. 6) op de grootte van de eerste worp.

Onderzoekingen werden opgezet om de invloed van het standaardisatieniveau (toomgrootte tijdens de zoogperiode) op de ontwikkeling van de gelt, de leeftijd bij eerste bronst, de grootte van de eerste worp en het aantal corpora lutea na de eerste bronst bij eerste worpszeugen te bepalen. Het effect van maternale invloeden op de te verwachten selectierespons werd met behulp van Monte Carlo simulatie bestudeerd. Drie generaties Nederlands Landvarken gelten werden opgefokt. De eerste generatie (192 gelten) werd aangekocht. De door deze gelten geproduceerde eerste worps tomen werden binnen 24 uur gestandaardiseerd op 8 biggen per worp. De tomen die geproduceerd werden door gelten van de tweede generatie werden gestandaardiseerd op 12 (hoog) of 6 (laag) biggen. Het effect van het standaardisatie niveau op produktie- en reproduktiekenmerken kwam dus tot uitdrukking bij gelten van de derde generatie die waren opgegroeid in grote of kleine tomen. Gelten werden geïnsemineerd op een leeftijd van gemiddeld 255 dagen.

De groei van biggen van geboorte tot spenen (op een leeftijd van 5 weken) in grote tomen was 24% lager dan die van biggen in kleine tomen. Van spenen tot een leeftijd van 56 dagen was het verschil in groei 8%, ten gunste van biggen uit de kleine tomen. Dit resulteerde in gewichten op een leeftijd van 56 dagen van 15,8 en 18.7 kg voor biggen die waren opgegroeid in respectievelijk grote en kleine tomen. De opname van energie per big via de melk was 26% lager op het hoge in vergelijking met het lage niveau. De opname van metaboliseerbare energie gedurende de periode van 21 tot 35 dagen na geboorte via melk en babybiggenkorrel was 19% lager (table 5.1). De relaties tussen de opname van melk en/of babybiggenkorrel enerzijds en de groei tijdens de zoogperiode anderzijds kwamen op het hoge standaardisatie niveau duidelijker naar voren dan op het lage niveau. De melkproduktie op het hoge niveau vormt een beperkende factor voor de groei tijdens de zoogperiode.

Het significante gewichtsverschil op 56 en 74 dagen tussen gelten, opgegroeid in grote en kleine tomen, was op het moment van inseminatie verdwenen. De spekdikte, gemeten bij een gewicht van ca. 100 kg, was hoger bij gelten uit de grote tomen. Van de hoge standaardisatie niveau gelten die een toom produceerden werd 20% geinsemineerd bij de eerste bronst. Bij gelten van het lage niveau was dit 49%. Dit resultaat werd bereikt ondanks het feit dat er geen verschillen in leeftijd bij eerste bronst en drachtigheidspercentage na eerste inseminatie bestonden tussen beide groepen gelten. Een interactie tussen standaardisatie niveau en bronstnummer bij inseminatie op drachtheidspercentage speelde hierbij een rol. Van de 111 gelte van generatie drie, die een toom produceerden, waren er 96 halothaan negatief. Binnen deze laatste groep was het verschil in worpgrootte (totaal aantal geboren biggen), na correctie voor het effect bronstnummer bij inseminatie, 0,48 biggen ten gunste van het lage standaardisatie niveau (table 5.5). Het gerealiseerde verschil in standaardisatie niveau tussen beide groepen bedroeg 5,4 biggen. Dit leverde een "m-waarde" op van -0,09 (= -0,48/5,4). De coëfficiënt m is de partiële regressiecoëfficiënt van de fenotypische waarde van de dochter op de fenotypische waarde van de moeder voor het kenmerk worpgrootte in de afwezigheid van genetische verschillen tussen de moeders. Deze m-waarde kan worden opgesplitst in een pre- en postnatale component m_1 en m_2 ($m = m_1 + m_2$). Gelten opgegroeid in kleine tomen hadden zwaardere en langere uterushoornen (na de eerste bronst na het spenen van de eerste worp) dan die opgegroeid in grote tomen. Het aantal corpora lutea was hierbij hoger voor gelten van het lage niveau (table 4.28).

Op grond van de gevonden resultaten werd de conclusie getrokken dat het lage standaardisatie niveau een positieve invloed uitoefende op het speengewicht en de ontwikkeling van de uterus. Dit zou, in combinatie met een grotere voorraad van primordiale follikels in de ovaria, het gunstige effect op de toomgrootte kunnen verklaren.

Met behulp van een simulatiestudie en afgeleide formules werden de genetische implicaties van maternale invloeden op worpgrootte bestudeerd. Dochter-moeder regressiecoëfficiënten en in mindere mate kleindochter-grootmoeder regressiecoëfficiënten worden beïnvloed door maternale effecten (fig. 5.5). De dochter-moeder regressiecoëfficiënt kan zelfs bij een redelijk hoge erfelijkheidsgraad voor worpgrootte negatief worden (bijv. $h^2 = 0,2$; $m \leq -0,10$). De postnatale maternale invloed, voor zover die bepaald wordt door de toomgrootte tijdens de zoogperiode, kan worden opgeheven door het standaardiseren van tomen na de geboorte.

Maternale effecten beïnvloeden de selectierespons op twee manieren. In de eerste plaats wordt de regressiecoëfficiënt van additief genetische waarde op fenotypisch waarde beïnvloed. Een m-waarde van -0,1 of -0,2 verlaagt deze coëfficiënt, en daarmee de selectierespons, slechts met respectievelijk 5 en 11%. Verder veroorzaakt het maternale effect een belangrijke permanente milieu-invloed. Geselecteerde gelten zijn geboren en groeien op in grote tomen en ondervinden daardoor een negatieve maternale invloed. Deze negatieve permanente milieu invloed speelt geen rol bij selectie van beren uit de grootste tomen.

De negatieve invloed van maternale effecten op de selectierespons kan voor een deel worden opgeheven door het corrigeren van de gegevens en/of het standaardiseren van tomen. De afname van de regressiecoëfficiënt van additief genetische waarde op fenotypische waarde door maternale effecten kan worden opgeheven door het corrigeren van de fenotypische waarden . Hiervoor moeten we beschikken over nauwkeurige schattingen van m_1 en m_2. Het is twijfelachtig of deze correctie nuttig is omdat de invloed op deze regressiecoëfficiënt beperkt is. Het standaardiseren van tomen is effectiever omdat hierdoor zowel de verlaging van genoemde regressiecoëfficiënt als de permanente negatieve milieu-invloed veroorzaakt door postnatale maternale effecten worden opgeheven.

Een negatieve dochter-moeder regressiecoëfficiënt voor worpgrootte (veroorzaakt door maternale effecten) impliceert niet dat het selecteren van opfokgelten, die zijn geboren en opgegroeid in grote tomen, geen selectierespons voor worpgrootte kan opleveren. Het is namelijk de waarde van de regressiecoëfficiënt van fokwaarde op fenotypische waarde die van belang is. Een vrij extreme waarde voor de maternale invloed ($m = -0{,}20$) levert slechts een verlaging van deze coëfficiënt, en dus de genetische vooruitgang, van 11% op.

De genoemde negatieve permanente milieu invloed is, genetisch gezien, niet van belang maar veroorzaakte wel een verlaging van de fenotypische waarde van de worpgrootte hetgeen, economisch gezien, een nadeel oplevert. Door deze invloed en door een te kleine opzet van een selectie-experiment of selectielijn kan de selectierespons, na enkele generaties van selectie op worpgrootte, niet waarneembaar zijn. Selectie-experimenten of -programma's, waarbij tomen worden gestandaardiseerd, resulteren in een toename van de worpgrootte of totale reproduktie capaciteit indien gewerkt wordt met populaties van voldoende omvang.

Voor het optimaliseren van de selectierespons moet aan de volgende aspecten nog aandacht worden besteed

- het bepalen van de economisch belangrijke componenten van de totale reproduktie capaciteit
- het verkrijgen van nauwkeurige schattingen van de relevante genetische en fenotypische correlaties en erfelijkheidsgraden
- het combineren van de bronnen van informatie in een index en

- het bepalen van de optimale selectiestrategie.

Het niet toenemen van de worpgrootte gedurende de laatste decennia is waarschijnlijk te wijten aan het ontbreken van selectiedruk. Een hogere selectiedruk in combinatie met efficiëntere methoden (populaties van voldoende omvang, het standaardiseren van tomen, nauwkeurig verzamelen van gegevens, combineren van informatiebronnen in een index) toegepast gedurende een periode van 10 jaar of meer leidt tot een selectierespons die van economisch belang is.

Appendix 1 Formulation of the feed

Sow feed

Ingredients	Mass fraction (%)
Maize	12
Barley	18
Soya bean oilmeal (with 44-47% crude protein)	15
Pollards	15
Tapioca pellets	13
Maize gluten feed	5
Lucerne meal	8
Citrus pulp	5.5
Animal fat	1.1
Molasses	5
Minerals/vitamins premix*	2
Calcium hydrogen phospate	0.4

* Guaranteed contents: Ca 253 g/kg, P 75 g/kg, Na 60 g/kg, Cu 500 mg/kg, Fe 4000 mg/kg, Zn 2000 mg/kg, Mn 1200 mg/kg, Co 12.5 mg/kg, J 20 mg/kg, Se 2.5 mg/kg, 35000 μg retinol equivalent/kg, 1750 μg Cholecalciferol equivalent/kg, riboflavin 175 mg/kg, 900 mg nicotinamide equivalent/kg, pantothenic acid 350 mg/kg, choline 12500 mg/kg, vitamin B-12 0.75 mg/kg, 235 mg α-tocopherol equivalent/kg, dl methionine 10 g/kg.

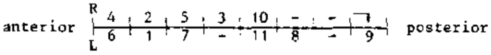
Composition of the feed as analysed and calculated. Values are mass fractions in fresh matter (%).

	By analysis (mean ± standard deviation)	By calculation (CVB 1979)
Dry matter	87.64 ± 0.67	87.45
Ash	6.59 ± 0.43	7.22
Crude protein	15.11 ± 0.64	15.87
Crude fat	3.26 ± 0.56	3.40
Crude fibre	7.09 ± 0.46	6.74
Gross energy content (MJ/kg)	15.86 ± 1.66	
Net energy content (MJ/kg) by Rostock equation		8.57

Appendix 2

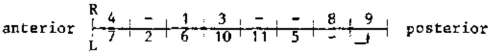
Calculation of the teat order litter score (TOSA) and the average teat number suckled by a piglet (an example).

First suckling



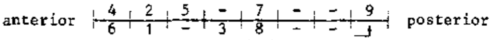
position of the sow: on right side

Second suckling



position of the sow: on left side

Third suckling



position of the sow: on right side

piglet number	case	calculation	score	average teat number
4	1	10	10	1
2	2a	9-X; X=1-1=0	9	2
5	2a	9-X; X=4-1=3	6	3
1	2a	9-X; X=2-1=1	8	2
3	2b	9-X; X=1	8	4
6	2b	9-X; X=2	7	1
7	3	$6-X_1-X_2$; $X_1=2$, $X_2=3$ teat 3L is the main teat	1	3
8	3	$6-X_1-X_2$; $X_1=1$, $X_2=2$ teat 6L is the main teat	3	5
9	special	pig suckling both teats		8
10	4a	$6-2-X_1$; $X_1=2$	2	5
11	4b	9-4	5	5

Appendix 3 Generation and period least squares means for weights and growth up to 56 days of age (litter means; model I).

Variable	Generation			period			
	2	3	4	1	2	3	4
Weight (kg)							
AW0b	1.27	1.36	1.36	1.34	1.34	1.29	1.34
AW0s	1.31	1.39	1.38	1.36	1.38	1.33	1.37
AW21	5.82	5.62	5.90	5.65	6.07	5.87	5.53
AW35	9.20	9.44	9.55	9.11	9.71	9.63	9.13
AW56	17.88	17.19	16.20	16.49	17.48	17.24	17.16
Growth (g/d)							
AG0-35d	223	230	233	220	238	235	221
AG35-56d	413	368	314	350	369	360	380

Appendix 4 Generation and period least squares means of growth and weight from 74 days of age to parturition and backfat thickness, relations with age and weight and the significance level of Ge, Per, Ge*Per, STL and covariables (model I).

Variable	Least squares means							Significance levels				Covariables				
	Ge1	Ge2	Ge3	Per1	Per2	Per3	Per4	Ge	Per	Ge*Per	STL		b	P	r.s.d.	R²
Weight (kg)																
W74	23.3	26.0	24.7	25.1	25.5	24.3	23.7	0.00	0.00	0.08	0.00	AW74	0.522	0.00	3.3	0.56
W130	57.9	57.3	57.2	58.0	57.5	57.2	57.2	0.58	0.65	0.00	0.02	AW130	0.629	0.00	6.0	0.37
W214	110.1	104.5	107.5	108.3	105.4	105.2	110.5	0.00	0.00	0.00	0.38	AW214	0.626	0.00	9.3	0.24
WIN	123.8	124.9	126.3	126.0	120.3	125.3	128.4	0.08	0.00	0.52	0.32	AIN	0.440	0.00	8.6	0.30
WEI	126.2	128.1	129.7	128.4	123.2	128.6	131.9	0.02	0.00	0.76	0.45	AEI	0.325	0.00	8.8	0.34
WBP	187.3	189.2	198.2	187.3	187.0	192.2	199.9	0.00	0.00	0.58	0.03	ABP	0.428	0.00	10.3	0.45
WAP	170.8	171.5	180.0	170.7	170.4	175.1	180.3	0.00	0.00	0.56	0.05	AAP	0.406	0.00	9.7	0.41
Growth (g/d)																
G25-100k	638	568	598	613	573	590	630	0.00	0.00	0.01	0.03	A25k	-2.28	0.00	62	0.25
G70k-IN	505	509	524	513	481	517	539	0.01	0.00	0.00	0.52	A70k	-0.25	0.24	53	0.20
Weight difference (kg)																
W214-W74	86.1	78.1	82.5	82.9	78.4	81.0	86.7	0.00	0.00	0.15	0.05	AW74	-0.156	0.08	8.3	0.20
												W74	0.506	0.00		
WBP-WIN	63.2	64.5	72.1	61.9	66.9	66.8	70.8	0.00	0.00	0.03	0.04	AIN	-0.032	0.53	6.3	0.47
												WIN	-0.051	0.27		
WAP-WIN	46.7	46.7	54.0	45.3	50.1	49.7	51.4	0.00	0.00	0.03	0.08	AIN	-0.029	0.52	5.8	0.42
												WIN	-0.096	0.02		
Backfat thickness (mm)																
BFA	12.23	11.79	11.59	12.36	11.42	11.66	12.02	0.02	0.00	0.00	0.11	ABFA	0.02	0.18	1.91	0.39
												W186	0.13	0.00		
BFW	12.90	12.46	11.71	12.94	11.96	11.98	12.54	0.00	0.00	0.01	0.07	ABFW	-0.02	0.00	1.78	0.21
												W100k	0.11	0.00		

Appendix 5 Influence of standardization level and halothane susceptibility upon weight, growth and backfat thickness during the rearing period (model II).

Variable	Least squares means STL_H	STL_L	HAL_{neg}	HAL_{pos}	STL (H-L)	P	HAL (neg-pos)	P	r.s.d.	R²	covariables included in the model
Weight (kg)											
W74	23.0	25.8	25.2	24.6	-2.7	0.00	0.6	0.18	3.2	0.61	AW74
W130	55.5	57.5	57.1	54.8	-2.0	0.02	2.3	0.01	5.6	0.40	AW130
W214	105.3	106.4	106.6	102.1	-1.1	0.42	4.5	0.00	9.2	0.30	AW214
WIN	124.6	125.9	126.7	122.9	-1.3	0.35	3.8	0.01	8.7	0.34	AEI
WEI	129.2	130.1	131.1	127.7	-0.9	0.50	3.5	0.01	9.0	0.24	AIN
WBP	194.7	198.9	195.4	190.5	-4.2	0.05	4.9	0.04	10.9	0.38	ABP
WAP	177.7	181.4	177.1	174.6	-3.7	0.07	2.5	0.25	10.4	0.33	AAP
Growth (g/d)											
G25-100k	602	580	586	563	22	0.01	22	0.01	57	0.29	A25k
	593	583	587	562	10	0.25	25	0.00	58	0.24	---
G70k-IN	524	518	524	516	6	0.44	7	0.36	50	0.17	A70k
	523	518	524	515	5	0.55	9	0.24	50	0.16	---
Weight difference (kg)											
W214-W74	83.2	80.1	81.4	77.8	3.1	0.01	3.5	0.00	7.8	0.29	AW74, W74
	82.1	80.5	81.5	77.6	1.6	0.17	3.9	0.00	8.0	0.26	AW74
WBP-WIN	70.6	72.8	68.6	67.9	-2.2	0.09	0.7	0.63	6.8	0.31	AIN, WIN
	70.6	72.8	68.6	67.9	-2.2	0.09	0.7	0.63	6.7	0.31	AIN
WAP-WIN	53.5	55.3	50.3	51.8	-1.8	0.13	-1.5	0.24	6.1	0.31	AIN, WIN
	53.6	55.3	50.2	51.9	-1.7	0.14	-1.7	0.19	6.0	0.31	AIN
Backfat thickness (mm)											
BFA	11.28	10.79	11.86	10.71	0.50	0.03	1.14	0.00	1.56	0.49	ABFA, W186
	11.15	10.86	11.90	10.43	0.30	0.30	1.48	0.00	1.92	0.22	ABFA
BFW	11.59	11.01	12.29	11.24	0.58	0.03	1.06	0.00	1.77	0.19	ABFW, W100k
	11.55	11.05	12.31	11.10	0.50	0.06	1.20	0.00	1.80	0.15	W100k

Appendix 6 Standardization level * halothane susceptibility interaction upon weight, growth and backfat thickness (least squares means; model IIb + STL * HAL interaction effect).

Variable	covariable	HAL=negative		HAL=positive		HAL * STL
		STL_H	STL_L	STL_H	STL_L	P
Weight (kg)						
W74	AW74	23.2	25.5	22.0	26.6	0.15
W130	AW130	56.8	58.1	52.5	55.9	0.45
W186	AW186	91.1	91.4	83.2	88.5	0.19
WEI	AEI	131.3	131.3	123.1	129.9	0.08
WBP	-	197.7	200.8	190.8	197.0	0.67
WAP	-	179.3	182.1	172.8	179.2	0.57
W186-W74	AW74	67.9	65.9	61.2	61.9	0.37
WBP-WIN	AIN	70.6	73.3	70.8	72.6	0.83
Growth (g/d)						
G25-100k	-	614	594	546	563	0.14
Backfat thickness (mm)						
BFA	ABFA	11.94	11.49	9.79	9.68	0.70
BFW	ABFW	12.22	11.62	10.93	10.39	0.99
Number of gilts at WEI		78	73	13	10	

ntinuation of appendix 8

	Number of sample units
d.	Standard deviation
.d.	Residual standard deviation
	Determination coefficient $\left[\{\Sigma(y-\bar{y})^2-\Sigma(y-\hat{y})^2\}/\Sigma(y-\bar{y})^2\right]$
	Probability
tors	
	Generation
	Period
	Standardization level
	H = standardized at 12 piglets per litter
	L = standardized at 6 piglets per litter
	Halothane *susceptibility*
	neg = halothane non-susceptible
	pos = halothane *susceptible*
	Litter
I	Oestrus *number at insemination*
ND	Oestrus induction after weaning of the first litter
	sp = spontaneous oestrus
	ind = induced oestrus

Appendix 9 Heritability estimated by daughter-dam and granddaughter-granddam regression

Falconer (1965) and Alsing et al. (1980) did not distinguish between pre- and post-natal maternal effects. Pre-natal maternal influence is likely to be related to total number of piglets at birth (P_b). Post-natal maternal influence will be related to number of piglets at weaning as most piglet mortality occurs during the first 3 days of the suckling period. So the number of piglets weaned is highly correlated with the average number of piglets in a litter during the suckling period (P_s).

The maternal effect can be defined as the sum of pre-natal and post-natal maternal effect.

$$M = M_1 + M_2 = m_1 P'_b + m_2 P'_s \qquad (1)$$

The coefficient m_1 ia a partial regression coefficient relating the litter size of the daughter to the size of the litter at birth in which the daughter was born in the absence of genetic variation among the mothers, and in the absence of variatio in litter size during the suckling period. The partial regression coefficient m_2 is defined in a comparable way. These definitions exclude all maternal influences that are not related to the size of the litter. These, if present, will be include with the rest of the common environment in the C-component.

The phenotypic value of litter size at birth can be expressed as

$$P_b = A + M_1 + M_2 + R \qquad (2)$$

where $R = D + C + E$

(explanation of symbols, see section 2.1.2.2).

1. Heritability estimated by daughter-dam regression.

The phenotypic variance of litter size at birth can be written as

$$V_{P_b} = V_A + V_{M_1} + V_{M_2} + V_R + 2\,\mathrm{cov}(AM_1) + 2\mathrm{cov}(AM_2) + 2\,\mathrm{cov}(M_1M_2) \qquad (3)$$

because $\mathrm{cov}(AR)$, $\mathrm{cov}(M_1R)$ and $\mathrm{cov}(M_2R)$ are zero.

Phenotypic value of the mother is

$$P'_b = A' + M'_1 + M'_2 + R'$$

The covariance between daughter and dam $\{\mathrm{cov}(P_bP'_b)\}$ will be deduced first.

$$\mathrm{cov}(P_bP'_b) = \mathrm{cov}(AP'_b) + \mathrm{cov}(M_1P'_b) + \mathrm{cov}(M_2P'_b) + \mathrm{cov}(RP'_b) \qquad (4)$$

where $\mathrm{cov}(AP'_b) = \mathrm{cov}(AA') + \mathrm{cov}(AM'_1) + \mathrm{cov}(AM'_2) + \mathrm{cov}(AR')$

$$= \tfrac{1}{2} V_A + \mathrm{cov}(AM'_1) + \mathrm{cov}(AM'_2) \qquad (5)$$

assuming that the correlation between $G_{mn,w}$ (from equation 8 section 2.1.2.3) and A is zero.

$\mathrm{Cov}_{RP'_b}$ is zero because the daughters' D-, C- and E-deviations are uncorrelated with the mothers' phenotypic value.

$\mathrm{Cov}_{AR'}$ is zero because the daughters' breeding value is uncorrelated with the mothers' D-, C- and E-deviations.

P_b and P_s are expressed as deviations of the respective population means. P_s equals to P_b plus an additional deviation caused by variation in piglet mortality. So piglet mortality (Q) is defined as the deviation from the average piglet mortality.

$$P_s = P_b + Q \quad \text{where } \bar{Q} = 0$$

Under the assumption that piglet mortality is not genetically determined we can write

$$P_s = A + M_1 + M_2 + D + C + E + Q$$

$$= A + M_1 + M_2 + R^*, \quad \text{where } R^* = R + Q$$

For the purpose of deducing the covariance of M' with A, the terms R and R* can be omitted as they are not correlated with A. This is also only valid if the genetic correlation between $G_{mn,w}$ and A is zero. So the correlation between the additive genetic value for litter size, and the additive genetic value for traits which determine the maternal influence as far as it is not related to litter size was assumed to be zero. The derivations also hold if $G_{mn,w}$ is very small.
M'_1 can be written as $m_1P'_b$.
(Primes indicate ancestral generations: one prime indicates the parental generation, two primes indicate the grand-maternal generation etc.)

$$\begin{aligned} \text{so, } M_1' &= m_1(A'' + M_1'' + M_2'') \\ &= m_1(A'' + m_1(A''' + M_1''') + m_2(A''' + M_1''' + M_2''')) \\ &= m_1(A'' + (m_1 + m_2)(A''' + M_1''' + M_2''')) \\ &= m_1(A'' + (m_1 + m_2)(A''' + (m_1 + m_2)^2 (A'''' + \ldots\ldots \text{ etc.}) \end{aligned}$$

$$\begin{aligned} \text{and } \operatorname{cov}(AM_1') &= m_1 \operatorname{cov}(AA'') + m_1(m_1 + m_2) \operatorname{cov}(AA''') + m_1(m_1 + m_2)^2 \operatorname{cov}(AA'''') + \ldots\ldots \\ &= V_A(\tfrac{1}{4}m_1 + \tfrac{1}{8}m_1(m_1 + m_2) + \tfrac{1}{16}m_1(m_1 + m_2)^2 + \ldots\ldots \\ &= \tfrac{1}{4}m_1V_A\ (1 + \tfrac{1}{2}(m_1 + m_2) + \tfrac{1}{4}(m_1 + m_2)^2 + \ldots\ldots \\ &= \tfrac{1}{4}m_1V_A\ (1 + \frac{m_1 + m_2}{2 - m_1 - m_2}) \end{aligned} \qquad (6)$$

$$\operatorname{cov}(AM_2') = \tfrac{1}{4}m_2V_A\ (1 + \frac{m_1 + m_2}{2 - m_1 - m_2}) \qquad (7)$$

$$\operatorname{cov}(M_1P_b') = \operatorname{cov}(m_1P_b'\ ,\ P_b') = m_1V_{P_b'} \qquad (8)$$

$$\operatorname{cov}(M_2P_b') = \operatorname{cov}(m_2P_s'\ ,\ P_b') = m_2\ r\ V^{\frac{1}{2}}_{P_s'}\ V^{\frac{1}{2}}_{P_b'} \qquad (9)$$

where r = phenotypic correlation between P_b' and P_s'

Combining equations 4 to 9 gives

$$\operatorname{cov}(P_bP_b') = \tfrac{1}{2}\ V_A + \tfrac{1}{2}V_A(\frac{m_1 + m_2}{2 - m_1 - m_2}) + m_1\ V_{P_b'} + m_2\ r\ V^{\frac{1}{2}}_{P_s'}\ V^{\frac{1}{2}}_{P_b'} \qquad (10)$$

If $r = 1$; $V_{P_s'} = V_{P_b'}$ and $m = m_1 + m_2$

Then $\operatorname{cov}(P_bP_b') = V_A\ (\frac{1}{2 - m}) + m\ V_{P'}$ (equation 11; Falconer, 1965)

The covariance between daughters' and dams' litter size is reduced at negative values of $m_1 + m_2$. Maternal influences also affect the phenotypic variance (eq. 3). Equation 3 includes 5 terms which have to be expressed in terms of m_1 and/or m_2.

$$V_{M_1} = m_1^2\ V_{P_b'} = m_1^2\ V_{P_b} \qquad (11)$$

$$V_{M_2} = m_2^2\ V_{P_s'} = m_2^2\ V_{P_s} \qquad (12)$$

$$2\ \mathrm{cov}(AM_1) + 2\ \mathrm{cov}(AM_2) = 2\ V_A\ \left(\frac{m_1 + m_2}{2 - m_1 - m_2}\right) \tag{13}$$

$$2\ \mathrm{cov}(M_1M_2) = 2\ \mathrm{cov}\ (m_1P_b\ ,\ m_2P_s) = 2\ m_1m_2\ \mathrm{cov}(P_bP_s)$$

$$= 2\ m_1m_2\ r\ V_{P_b}^{\frac{1}{2}}\ V_{P_s}^{\frac{1}{2}} \tag{14}$$

Combining equations 3 and 11 to 14 with the assumption that $V_{P_b} = V_{P_s}$ and $r = 1$ gives

$$V_{P_b}\ (1 - m_1^2 - m_2^2 - 2\ m_1m_2) = V_A + V_R + 2\ V_A\ \left(\frac{m_1 + m_2}{2 - m_1 - m_2}\right)$$

for small values of m_1 and m_2 $\quad V_{P_b} \cong V_A + V_R$

e.g. $m_1 = m_2 = -0.05;\ V_A + V_R = 7;\ V_A/(V_A + V_R) = 0.1 \rightarrow V_{P_b} = 6.996$

or, $V_A/(V_A + V_R) = 0.2 \rightarrow V_{P_b} = 6.992$

$m_1 = m_2 = -0.10;\ V_A + V_R = 7;\ V_A/(V_A + V_R) = 0.1 \rightarrow V_{P_b} = 7.130$

or, $V_A/(V_A + V_R) = 0.2 \rightarrow V_{P_b} = 6.968$

Twice the daughter-dam regression coefficient gives

$$\hat{h}^2 = \frac{2\ \mathrm{cov}(P_b\ P'_b)}{V_{P'_b}}$$

$$\hat{h}^2 = h^{2*}.\ \frac{2}{(2 - m_1 - m_2)} + 2\ m_1 + 2\ m_2\ r\ (V_{P'_s}\ /\ V_{P'_b})^{\frac{1}{2}} \tag{15}$$

where $h^{2*} = V_A\ /\ V_{P'_b} \cong V_A/(V_A + V_R)$

If $V_{P'_s} = V_{P'_b}$ and $r = 1;\ m_1 + m_2 = m$

This reduces to

$$\hat{h}^2 = h^{2*}\ .\ \left(\frac{2}{2 - m}\right) + 2\ m \tag{16}$$

2. Heritability estimated by granddaughter-granddam regression

The estimated heritability equals $4 \operatorname{cov}(P_b P''_b) \, / \, V_{P''_b}$

where $\operatorname{cov}(P_b P''_b) = \operatorname{cov}(AP''_b) + \operatorname{cov}(M_1 P''_b) + \operatorname{cov}(M_2 P''_b) + \operatorname{cov}(RP''_b)$

$$\operatorname{cov}(AP''_b) = \operatorname{cov}(AA'') + \operatorname{cov}(AM''_1) + \operatorname{cov}(AM''_2) + \operatorname{cov}(AR'')$$

$$= \tfrac{1}{4} V_A + \operatorname{cov}(AM''_1) + \operatorname{cov}(AM''_2) \quad \text{, since } \operatorname{cov}(AR'') \text{ is zero}$$

$$\operatorname{cov}(AM''_1) = \tfrac{1}{8} m_1 V_A \left(1 + \frac{m_1 + m_2}{2 - m_1 - m_2}\right)$$

$$\operatorname{cov}(AM''_2) = \tfrac{1}{8} m_2 V_A \left(1 + \frac{m_1 + m_2}{2 - m_1 - m_2}\right)$$

$$\operatorname{cov}(M_1 P''_b) = \operatorname{cov}(m_1 P'_b \, , \, P''_b) = m_1 \operatorname{cov}(P'_b \; P''_b)$$

$$\operatorname{cov}(M_2 P''_b) = \operatorname{cov}(m_2 P'_s \, , \, P''_b) = m_2 \operatorname{cov}(P'_s P''_b) = m_2 \operatorname{cov}(P'_b P''_b)$$

$$= m_2 \operatorname{cov}(P'_b + Q' \, , \, P''_b) = m_2 \operatorname{cov}(P'_b P''_b)$$ since it was assumed that piglet mortality is not genetically determined.

so, $$\operatorname{cov}(P_b P''_b) = \tfrac{1}{4} V_A + \tfrac{1}{8} V_A \left(1 + \frac{m_1 + m_2}{2 - m_1 - m_2}\right)(m_1 + m_2) + (m_1 + m_2) \operatorname{cov}(P'_b P''_b)$$

$$= \tfrac{1}{4} V_A \left\{ \frac{2}{2 - m_1 - m_2} \right\} + (m_1 + m_2) \operatorname{cov}(P'_b P''_b)$$

combining this with equation 10 gives:

$$\operatorname{cov}(P_b P''_b) = \tfrac{1}{4} V_A \left\{ \frac{2}{2 - m_1 - m_2} \right\} + (m_1 + m_2)\{ \tfrac{1}{2} V_A + \tfrac{1}{2} V_A (\frac{m_1 + m_2}{2 - m_1 - m_2}) +$$

$$m_1 V_{P''_b} + m_2 \, r \, V^{\frac{1}{2}}_{P''_s} V^{\frac{1}{2}}_{P''_b} \}$$

$$= V_A \left(\frac{\frac{1}{2} + m_1 + m_2}{2 - m_1 - m_2}\right) + (m_1 + m_2)\{ m_1 V_{P''_b} + m_2 \, r \, V^{\frac{1}{2}}_{P''_s} V^{\frac{1}{2}}_{P''_b} \}$$

so, $$\hat{h}^2 = 4 \, b_{P_b P''_b} = 4 \; \frac{\operatorname{cov}(P_b P''_b)}{V_{P''_b}}$$

$$= \frac{V_A}{V''_P} \left(\frac{2 + 4 (m_1 + m_2)}{2 - m_1 - m_2} \right) - 4 \, (m_1^2 + m_1 m_2 + (m_1 + m_2) \, m_2 \, r \, V^{\frac{1}{2}}_{P''_s} V^{-\frac{1}{2}}_{P''_b} \qquad (17)$$

f $m_1 + m_2 = m$; $V_{P''_s}$; $V_{P''_b}$; $r = 1$

hen $\hat{h}^2 = \frac{V_A}{V_{P''}} \frac{2 + 4m}{2 - m} + 4m^2 \cong h^{2*} \frac{2 + 4m}{2 - m} + 4m^2$ (18)

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CURRICULUM VITAE

H.A.M. van der Steen werd geboren op 19 augustus 1952 te Veghel. Na het behalen van het einddiploma HBS-B aan het Mgr. Zwijsencollege te Veghel in 1969 begon hij in september van dat jaar met zijn studie aan de Landbouwhogeschool te Wageningen. Gedurende de ingenieursstudie was hij voor het hoofdvak en als onderdeel van de praktijktijd werkzaam bij Dr. M.J. Bryant aan de Universiteit te Reading (Engeland). Hij slaagde in juni 1975 met lof voor het doctoraal examen; verzwaard hoofdvak Gezondheids- en Ziekteleer met bijvakken Veeteelt, Dierfysiologie en Veevoeding. Vanaf juli 1975 is de auteur als wetenschappelijk medewerker verbonden aan de vakgroep Veefokkerij van de Landbouwhogeschool te Wageningen, met als onderzoeksterrein de genetische aspecten van de vruchtbaarheid van varkens.