Food intake capacity in relation to breeding and feeding of growing pigs

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Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C. C. Oosterlee,
in het openbaar te verdedigen
op vrijdag 19 februari 1988
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen.

STELLINGEN

1. De gangbare opvatting dat beperkter voeren samengaat met meer vlees in het karkas is onjuist indien een sterkere voerbeperking wordt gerealiseerd door bij dezelfde voergift het voeropnamevermogen van de dieren te verhogen.

   Dit proefschrift.

2. Genotype x milieu interacties tussen toets- en praktijkbedrijven worden o.m. veroorzaakt door beperkt voeren volgens normen die geen rekening houden met variatie in voeropnamevermogen.

   Dit proefschrift.

3. Selectie op mesterij- en slachtkenmerken met de huidige selectie indices heeft tot gevolg dat het optimale voerniveau voor vleesvarkens steeds dichter bij ad libitum komt te liggen.

   Dit proefschrift.

4. Het risico dat door index-selectie op mesterij- en slachtkenmerken het voeropnamevermogen afneemt, geldt niet alleen voor selectie bij ad libitum voedering maar ook voor selectie bij beperkte voedering.

   Dit proefschrift.

5. De mogelijkheden die o.a. door Krieter (1986) worden genoemd om verdere teruggang van voeropnamevermogen te voorkomen, zijn niet voldoende onderbouwd.

   Krieter, J., 1986. Entwicklung von Selektionsmethoden für das Wachstums- und Futteraufnahmevermögen beim Schwein. Ph.D. Thesis, Christian-Albrechts-University, Kiel.

6. De balans tussen selectie op produktie- en reproduktiekenmerken slaat momenteel teveel door naar de eerste categorie.

7. Bij het ontwikkelen en toepassen van groeimodellen voor varkens wordt het belang van variatie tussen dieren onderschat.

8. Het gebruik van desired gains indices voor selectie zal toenemen naarmate de kennis van fysiologische processen in het dier toeneemt.

9. Door de modernisering van de classificatie van geslachte varkens is het gevaar vergroot dat er teveel gestreefd wordt naar een zo hoog mogelijk vleespercentage.

10. De achterstand van de visfokkerij op de fokkerij van andere landbouwhuisdieren kan in korte tijd worden ingelopen door toepassing van nieuwe genetische technieken in combinatie met kwantitatieve genetica.

11. Stimulering van onderzoek naar effecten van toediening van, via recombinant-DNA technieken verkregen, dierlijke produkten is van essentieel belang voor een goede onderbouwing van het beleid inzake toepassing van biotechnologie in de dierlijke produktie.

12. Onderzoekfondsen van vakgroepen van de Landbouwuniversiteit worden door de afdeling Financiële en Economische Zaken teveel gebruikt als melkkoe.

13. Het vroegtijdig vaststellen van een promotiedatum is een vorm van zelfbescherming.

14. Door te verwachten dat met de instelling van de categorie „niet-rijdend lid" de ruimte voor nieuwe leden van de vereniging „De Friesche Elf Steden" aanzienlijk zal toenemen, geeft het bestuur van deze vereniging er blijk van niet op de hoogte te zijn met de diepste wens van haar leden.

15. Een wet die er van uitgaat dat men met twee glazen bier op nog veilig kan rijden vraagt om ongelukken.

Proefschrift van Egbert Kanis
Food intake capacity in relation to breeding and feeding of growing pigs.
Wageningen, 19 februari 1988.

VOORWOORD

Dit proefschrift is het resultaat van onderzoek gedaan bij de vakgroep Veefokkerij van de Landbouwuniversiteit. Een deel van de proeven werd uitgevoerd in samenwerking met de vakgroep Veehouderij, de vakgroep Experimentele Diermorfologie en Celbiologie, het IVO "Schoonoord" in Zeist, het IVVO in Lelystad en het Laboratorium voor Diervoedingsleer van de Rijksuniversiteit te Gent (België). De brede opzet en het experimentele karakter van dit onderzoek betekenen per definitie dat velen hebben bijgedragen aan de totstandkoming van dit proefschrift. Graag wil ik alle betrokkenen bedanken voor hun bijdrage. Enkelen wil ik wat naar voren halen.

De eerste proeven waarop dit proefschrift mede is gebaseerd, zijn nog ontworpen door bewoners van het toenmalige "pig department" aan het Duivendaal. Hun ideeën hebben een sterke invloed gehad op de opzet van de daarop volgende proeven. De uitvoering vond plaats op de proefaccommodatie "De Haar varkens en kalveren". Met name André Jansen, Sjaak Tijnagel en Ries Verkerk wil ik bedanken voor de goede verzorging van de varkens.

De organisatie van de proeven, het verzamelen van de vaak omvangrijke hoeveelheden gegevens alsmede de gedeeltelijke verwerking daarvan werd vakkundig en nauwgezet uitgevoerd door Piet de Groot, Jan Souman en Klaas de Roo. Hun inzet en betrokkenheid bij het onderzoek heeft een positieve invloed gehad op de kwaliteit van de resultaten. Ook studenten van Hogere Agrarische Scholen en Landbouwuniversiteit ben ik erkentelijk voor hun bijdragen aan het onderzoek en voor de verwerking van onderdelen daarvan.

Een "klankbordgroep" is vrijwel onmisbaar voor de goede afronding van een proefschrift. De opbouwende kritiek van Wiebe Koops, Hein van der Steen, Martin Verstegen en Alfred de Vries naar aanleiding van de manuscripten vond ik bijzonder waardevol. De figuren werden getekend door Wout Heije en Klaas Boekhorst. Van het Engels werd English gemaakt door Mike Grossman en Gary Rogers. Allemaal hartelijk bedankt!

Mijn promotor, prof.dr.ir. R.D. Politiek ben ik erkentelijk voor zijn geduld en stimulerende invloed, alsook voor de vrijheid die mij binnen de vakgroep Veefokkerij werd gegeven om dit proefschrift af te ronden.

Tot slot dank ik het LEB-fonds voor de bijdrage in de kosten van dit proefschrift.

Egbert Kanis

CONTENTS

INTRODUCTION

A pig converts food into body components by means of a complex system of well balanced biological processes. Food should contain the energy, protein and other nutrients needed for maintenance and for production and deposition of protein and fat. In growing pigs, most protein is deposited in muscles (Metz et al., 1984). However, a considerable part of the protein is deposited in less edible body components, such as intestines, skin, hair and claws. Most fat is deposited as subcutaneous, abdominal or inter- and intra-muscular fat. The rate of protein and fat deposition determines to a large extent the level of production traits, such as daily gain, food conversion ratio and body composition.

Amount of food eaten by a pig has great influence on rate of protein and fat deposition and, consequently, on the level of production. Food intake may be determined by the pig producer (restricted feeding) or by the animal itself (ad libitum feeding). In the latter case, the food intake capacity of the animal is important for production.

A high food intake has a positive effect on rate of body-weight gain, but this is not always favourable in an economic sense. If food intake exceeds food needed for maximum rate of protein gain, extra fat will be produced. Extra fat production is associated with an unfavourable food conversion ratio and a lower carcass quality. Therefore, growing pigs are often fed at a restricted feeding level during part of the growing period.

A low food intake, however, can be unfavourable as well, if the capacity to produce protein is not fully used and the proportion of food energy required for maintenance becomes too high.

Selection in growing pigs has been mainly for a combination of daily gain, food conversion ratio and carcass composition. There is evidence that selection programmes that give most emphasis to a low food conversion ratio and a high proportion of lean meat in the carcass, at the expense of growth, can lead to reduction in food intake capacity, especially with testing under ad libitum feeding (Webb and Curran, 1986). This reduction is undesirable if it limits further increase of lean tissue growth rate. Therefore, food intake capacity should be a trait to consider in the breeding goal. However, it is not clear how best to combine selection for food intake capacity and production traits (Krieter, 1986; Brandt, 1987).

This thesis is focused on relationships of food intake and food intake capacity with production traits: average daily body-weight gain, food conversion ratio, backfat thickness, proportion and gain of lean and fatty tissue and lean tissue food conversion. Implications of variation in food intake capacity for breeding and feeding strategies will be discussed. Most results and conclusions are based on a series of experiments with growing pigs (barrows and gilts) carried out at the experimental unit "De Haar" of the Wageningen Agricultural University. In each experiment, animals were housed individually and fed at different feeding levels. The litter structure was part of the experimental design.

In chapter 1, relationships between average daily food intake and average levels of production traits during the growing period are described.

Food intake capacity can be defined as the average voluntary food intake per day during the growing period. For animals fed at a restricted feeding level, food intake capacity can be estimated, for instance on the basis of ad libitum food intake of littermates. Relationships among estimated food intake capacity and production traits are in chapter 2.

It has been shown recently that genetic correlations of production traits in test-stations with production traits in commercial environments are unexpectedly low (e.g. Merks, 1988). The importance of differences in food intake capacity for this type of genotype by environment interactions is discussed in chapter 3.

In chapter 4, time courses of daily body-weight gain, daily food intake and food efficiency during the growing period, as well as their interrelationships, are described.

Chapter 5 contains a biological model to describe production traits as a function of a pig's protein deposition capacity and of its food intake capacity. The model is used to estimate economic values of food intake capacity and protein deposition. Ways to optimize selection for food intake capacity in conjunction with selection for production traits are presented and discussed.

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CHAPTER 1

EFFECT OF AVERAGE DAILY FOOD INTAKE ON PRODUCTION PERFORMANCE IN GROWING PIGS

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Accepted for publication in Animal Production.
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ABSTRACT

Effects of daily food intake (FI) on daily gain (DG), food conversion ratio (FCR), ultrasonic backfat thickness (BF), percentage lean parts (LP), percentage fatty parts (FP), lean tissue growth rate (LTGR), fatty tissue growth rate (FTGR) and lean tissue food conversion (LTFC) were investigated in 687 barrows and 98 gilts, slaughtered at a mean live weight of 108 kg and fattened in seven batches. In the range of food intake from about 1.7 to 3.2 $kg.d^{-1}$ (22 to 42 MJ digestible energy) a continuous distribution of data was available.

Body composition was linearly related to FI. Most regressions of BF and all of LP and of FP on FI were linear, showing fatter animals at higher food intake. For FTGR, BF, LP and FP, parameter estimates based on linear regression were given. Although the response of DG and of LTGR on increasing FI was not always significantly different from linearity, the second degree polynomials indicated diminishing returns in all batches. FTGR had a high linear correlation with FI (0.85 to 0.95), indicating that in the present range of FI a rather fixed proportion of the food for production was used to deposit fatty tissue.

For DG and LTGR a non-linear model of the type $a(FI-f_0)^b$ was fitted, where f_0 was interpreted as maintenance requirement. For FCR and LTFC the corresponding model was $FI/(a(FI-f_0)^b)$. Both models were preferred over quadratic polynomials because of better interpretation of parameters. FCR and LTFC showed minima at FI of about 2.6 and 2.2 $kg.d^{-1}$, but especially for FCR the increase at increasing FI was low. Results were not consistent in demonstrating or refuting a plateau in LTGR, which in any event appears to lie near to or beyond ad libitum FI for most pigs.

INTRODUCTION

Relations between average daily food intake (FI), either ad libitum or restricted, and production traits in growing pigs have been the subject of many studies. This is justifiable because food intake is a major component in variation of production traits.

In the literature there is good agreement on the direction of the effects of food intake. Results concerning the shape of relationships however, are less consistent. Reviews by Vanschoubroek et al. (1967) and Fuller (1971) showed a diminishing return response of daily live-weight gain (DG) to increasing FI, whereas the Agricultural Research Council (ARC, 1981) concluded the response was linear.

Food conversion ratio (FCR; kg food consumed per kg of live-weight gain) showed a minimum at about 75% of ad libitum intake (Vanschoubroek et al., 1967; Davies and Lucas, 1972). Results of Fuller (1971) indicated that FCR was only slightly influenced by FI in the range of 1.6 to 2.6 $kg.d^{-1}$. Barber et al. (1972), Berg (1976) and Denissen (1979) found that in healthy pigs, with a good genetic background for meat production, ad libitum feeding did not have negative consequences for FCR. However, Campbell et al. (1985) found curvilinear relationships between DG and FI and between FCR and FI in 20 entire males and 20 females growing from 48 to 90 kg live weight. Minimum FCR was at 33 MJ digestible energy (DE) intake per day, being about 79% of ad libitum for males and 84% for females.

The response of backfat thickness (BF) to increasing FI appears to be not significantly different from linearity (Vanschoubroek et al., 1967; Fuller, 1971; ARC, 1981).

The relation between FI and protein retention or lean tissue growth rate (LTGR) is not clear. At low feeding levels, a linear response to increasing FI is mostly accepted, whereas at higher feeding levels a plateau or a limit in LTGR may appear (Fuller, 1971; Whittemore and Fawcett, 1976; ARC, 1981; Whittemore, 1983 and 1985). Campbell et al. (1985) found maximum protein deposition in pigs growing from 48 to 90 kg live weight at an intake of 33 MJ $DE.d^{-1}$ for each sex. They concluded that response was of a linear/plateau form. Whittemore (1985) too accepted the linear/plateau concept for LTGR. ARC (1981) reviewed experiments with pigs growing from about 20 kg to 105 kg, which suggested some curvilinearity, particularly at the higher food intakes. However, most food intake data in the ARC study did not exceed 30 MJ metabolizable energy per day. Nevertheless it was concluded that a linear model was the best empirical description of the data over a wide range of food intake, especially for young pigs of high potential on good diets (ARC, 1981).

Before the plateau in protein retention is reached, fat retention seems to be proportional to protein retention; thus a linear relation between fatty tissue growth rate (FTGR) and FI may be expected (Whittemore, 1983). At a higher FI, an increasing amount of energy is available for fat production, causing an accelerating FTGR.

The level of a plateau in LTGR, as well as the FI at which that plateau appears, depends among others on sex and genotype of the pigs. In pig breeding, much attention has been paid to improvement of production traits and, more recently, to the possible consequences of selection for production traits on the voluntary food intake in pigs (Standal and Vangen, 1985; Brandt et al., 1985). It seems possible that selection has altered relations between FI and production traits. This may be an important reason for discrepancies in the literature concerning the shape of relationships between FI and production traits. Developments in housing and management, feeding systems and food composition also create new needs for actual knowledge on relations between FI and production traits. The aim of this paper is to investigate these relationships for a continuous range of average daily food intake as applied in normal pig fattening practice.

MATERIAL AND METHODS

Animals and housing

Results concern production traits of 687 barrows and 98 gilts fattened in 6 experiments from 1976 to 1982 at the Agricultural University experimental station De Haar. Pigs were crossbreds between Dutch Yorkshire and Dutch Landrace, housed and fed individually. Animals in experiments 1 to 5 were barrows, whereas those in experiment 6 were barrows and gilts from the same litters. Each experiment was considered as one batch, except experiment 6 where barrows and gilts were considered as two separate batches. The growing period was, on average, from 27 to 108 kg live weight. Pigs always had free access to water. Artificial light was provided during 12 hours per day and the temperature was kept within the zone of thermoneutrality. In some experiments, nitrogen balance trials were carried out and effects of hygiene and infections with endoparasites were studied. Effects of these treatments will not be reported here, but they did not influence the present conclusions, which are based on results within batches.

Feeding strategy and diets

Pigs were hand fed twice daily. Animals fed ad libitum never had empty troughs. Wastage of food was prevented by a grate over the troughs. Animals fed at a restricted level received food according to live weight. Food intake and live weight were recorded weekly. Lowest feeding level was 65% of ad libitum, which corresponds to 1.9 $kg.d^{-1}$ on average.

Each batch consisted of two to four feeding levels. In each batch, 20 to 100 animals were fed ad libitum, while the others (often litter mates of the ad libitum fed animals) were fed at a restricted feeding level according to a predetermined feeding strategy (Table 1). In batches 1 to 5, animals fed at a restricted feeding level were linked to one or two ad libitum fed animals and received a fixed proportion of the amount of food eaten by their ad libitum fed counterparts at similar live weights. By this design a considerable variation in FI was found, not only in the ad libitum fed animals, but also in the groups fed at a restricted level. In batches 6 and 7, animals were fed ad libitum until about 48 kg live weight, after which in each batch 67 animals were changed from ad libitum to restricted feeding according to a fixed scale on a live-weight basis.

Table 1. Numbers of animals and experimental characteristics, by batch, at start of the experiments.

	Batch						
	1	2	3	4	5	6	7
No. of animals	100	100	100	200	96	100	100
No. of litters	25	25	40	40	16	33	33
Sex (B=barrow, G=gilt)	B	B	B	B	B	B	G
Feeding levels (in % of ad libitum)	100 85 74 65	100 85 74 65	100 85 74	100 80	100 74	100 85[1)] 74[1)]	100 85[1)] 74[1)]
Animals per feeding level	25	25	40[2)]	100	48	33[3)]	33[3)]
Dissection method[4)]	1	1	1	2	2	1	1

1) Ad libitum until 48 kg live weight, scale feeding afterwards.

2) 20 animals fed ad libitum.

3) One feeding level with 34 animals.

4) See text.

The composition of the diet was constant within batches, but batches 1 to 4 were different from batches 5 to 7. In batches 1 to 4, the main food components in the dry matter ($g.kg^{-1}$) were: maize 400, barley 100, grain offals 180, millet 100, soy oil meal 90, fish meal 40, alfalfa 50, skimmed-milk powder 20, minerals and vitamins 20. This mixture contained 13.03 MJ digestible energy (DE), 162 g crude protein (CP) and 8.1 g lysine per kg. In batches 5 to 7 the dry matter components ($g.kg^{-1}$) were: maize 250, barley 100, soy oil meal 220, grain offals 135, tapioca 186, alfalfa 13, skimmed-milk powder 36, molasses 15, animal fat 17, minerals and vitamins 28. This mixture contained 13.41 MJ DE, 172 g CP and 9.4 g lysine per kg. To correct for the small difference in energy concentration of the food between batches, food intake in batches 5 to 7 was multiplied by 1.029.

Carcass composition

At the end of the growing period, BF was measured ultrasonically on four positions (Kroeske et al., 1968). Pigs were fasted one day before being slaughtered, which was one to seven days after the last weighing. Right carcass halves of pigs from batches 1, 2, 3, 6 and 7 were dissected according to Bergström and Kroeske (1968), referred to as method 1. Complete carcasses belonging to batches 4 and 5 were dissected according to a different method applied by a commercial slaughter factory (method 2). In batches 1, 2, 3, 6 and 7, the proportion of lean tissue was calculated as ham plus shoulder plus cutlets, all without subcutaneous fat, plus meat scraps, divided by the cold weight of that half. In the same way, the fatty tissue included subcutaneous fat from ham, loin, back and shoulder, plus belly, lard and backfat scraps. For batches 4 and 5, the proportion of lean tissue was calculated as ham plus shoulder (each including some subcutaneous fat) plus defatted loin in each carcass half, divided by the cold carcass weight. Fatty tissue included belly and backfat.

For calculation of tissue growth rates, the carcass weight at start of the growing period was taken as 0.7 times live weight (Walstra, 1980). The assumed proportion of lean tissue in the carcass at start of the growing period was taken, depending on the dissection method, as 0.6 in batches 1, 2, 3, 6 and 7 (P. Walstra, unpublished results) and 0.65 in batches 4 and 5. For fatty tissue, 0.15 and 0.10 were used as initial proportions in the carcass for the two clusters of batches, respectively.

Statistical analyses

Because of differences between batches, such as sex, year, season and average feeding level, results were analysed by batch. Polynomial regressions of DG, FCR, BF, percentage lean parts (LP) and fatty parts (FP), LTGR, FTGR and lean tissue food conversion (LTFC) on FI were fitted using the computer program BMDP5R (Dixon, 1983). *Goodness-of-fit of orthogonal polynomials* ($P<0.05$) was tested against the residual mean square from fitting a third degree polynomial. For graphical presentation the second degree polynomials were chosen for all traits.

In addition the following non-linear model was fitted for DG and LTGR:

$$y = a(FI - f_0)^b \qquad \text{(model 1)}$$

where y = DG or LTGR

a = proportionality coefficient (or value of y if $FI - f_0 = 1$)

f_0 = food intake at $y = 0$

b = exponent determining the bend of the curve

The corresponding model fitted for FCR and LTFC was:

$$y = \frac{FI}{a(FI - f_0)^b} \qquad \text{(model 2)}$$

where y is now FCR or LTFC. If $0<b<1$, model 2 has a minimum at $FI = f_0/(1-b)$. Models 1 and 2 have the advantage that they contain parameters that can be interpreted independently as biological traits (see Appendix).

RESULTS

Average daily food intake

Animals that died during the trials, or that had to be slaughtered before a live weight of 95 kg was reached, were excluded from the analyses. The number of animals per batch involved in the analyses, and some characteristics of FI are in Table 2. The chosen feeding strategy resulted in a wide range of FI. Within batches, the standard deviation in FI was high due to the different feeding levels and variation within feeding levels, which was related to the variation in the animals fed ad libitum. In batches 1 and 2 the highest individual intake was more than twice the lowest. Due to the relatively low ad libitum intake of gilts, the range in food intake in batch 7 was lower than in other batches. In all batches, except batch 5, good overlap in range of FI between feeding levels existed.

Table 2. Number of animals[1], means, standard deviations, and minimum and maximum values of food intake ($kg.d^{-1}$).

	Batch						
	1	2	3	4	5	6	7
No. of animals	99(99)	99(97)	100(83)	197(196)	92(89)	100(94)	98(93)
Mean	2.362	2.430	2.446	2.515	2.523	2.611	2.463
Stand. dev.	0.428	0.434	0.303	0.372	0.446	0.276	0.199
Minimum	1.686	1.641	1.992	1.910	1.897	2.219	2.111
Maximum	3.581	3.412	3.130	3.424	3.424	3.545	2.974

[1] No. of dissected animals in parentheses.

Polynomials

Means and standard deviations for production traits by batch are presented in Table 3. The variation in FI resulted in a considerable variation in production traits. Average DG, for the animals fed ad libitum, ranged from 0.873 $kg.d^{-1}$ (batch 7) to 0.975 $kg.d^{-1}$ (batch 2), with a corresponding range in FI of 2.539 to 3.001 $kg.d^{-1}$. This growth and food intake may be considered as quite high for commercial animals, which can be due partly to effects of crossbreeding and to the systems of housing (individually) and feeding (twice a day extra food in the troughs). Except for BF, LTGR and LTFC, the within-batch polynomial regressions of production traits on FI were significantly different.

In Table 4 the relations between FI and production traits are presented by means of the highest significant degree of orthogonal polynomial and the corresponding residual standard deviations (RSD). The value of d indicates the shape of the regression curves (d=0 to d=3: none, linear, quadratic or cubic). Except for LP, FP and FTGR, of which the relations never deviated significantly from linear, all production traits showed differences between batches in shape of the regression curves. BF deviated significantly from linear in only two batches. For both food conversion traits (FCR and LTFC) the relation with FI varied from being constant (d=0) to being cubic (d=3), however, with relatively high RSD values.

DG was highly correlated with FI but the relation was not always linear. Polynomials in three of the seven batches showed evidence for slightly, but significantly, diminishing increase of growth rates with increasing food intakes. In batch 3, even a cubic polynomial was significant, however, the decrease in RSD compared with linear was only 0.002 $kg.d^{-1}$.

Table 3. Means ($\bar{x}$) and standard deviations (s) for production traits.

		Batch						
		1	2	3	4	5	6	7
Daily gain ($kg.d^{-1}$)	$\bar{x}$	0.778	0.793	0.796	0.791	0.778	0.836	0.816
	s	0.160	0.165	0.113	0.129	0.145	0.103	0.088
Food conversion ratio	$\bar{x}$	3.062	3.095	3.089	3.196	3.258	3.137	3.036
	s	0.240	0.263	0.240	0.234	0.274	0.223	0.236
Backfat thickness (mm)	$\bar{x}$	16.52	16.89	16.95	14.86	16.05	16.01	12.89
	s	3.13	3.13	3.12	2.93	3.41	2.59	2.14
Lean parts (%)	$\bar{x}$	55.55	54.31	55.38	63.01	61.66	56.46	59.48
	s	3.75	3.33	2.96	1.81	2.40	2.83	2.41
Fatty parts (%)	$\bar{x}$	32.13	33.12	32.58	20.85	21.00	32.61	29.58
	s	3.77	3.45	3.09	1.64	2.02	2.83	2.37
Lean tissue growth rate ($kg.d^{-1}$)	$\bar{x}$	0.331	0.321	0.336	0.391	0.379	0.381	0.394
	s	0.058	0.060	0.047	0.058	0.066	0.052	0.045
Fatty tissue growth rate ($kg.d^{-1}$)	$\bar{x}$	0.232	0.239	0.236	0.153	0.155	0.258	0.224
	s	0.069	0.065	0.052	0.035	0.038	0.045	0.036
Lean tissue food conversion	$\bar{x}$	7.203	7.602	7.462	6.459	6.724	6.944	6.319
	s	0.964	0.974	0.808	0.549	0.771	0.807	0.697

Because generally, the quadratic polynomials fitted well, and an increasing or decreasing response of production traits to increasing FI is biologically well accepted, plots were based on quadratic polynomials (Figures 1 and 2). Thus, non-significant deviations from constancy or linearity become apparent. To avoid extrapolation, curves in Figures 1 and 2 were plotted for FI ranging from the mean in the group with the lowest feeding level minus its standard deviation to the mean in the ad libitum group plus its standard deviation.

Parameter interpretation

Only DG and LTGR uniformly showed tendencies for a decline in increase with increasing FI (Figures 1a and 1c). Therefore, models 1 and 2 seem to be suitable to fit to the data on DG, LTGR, FCR and LTFC. In Table 5, parameter

Table 4. Orthogonal polynomial regressions of production traits on average daily food intake ($kg.d^{-1}$): highest significant degree (d) and residual standard deviation (RSD)[1].

	Batch													
	1		2		3		4		5		6		7	
	d	RSD	d	RSD	d	RSD	d	RSD	d	RSD	d	RSD	d	RSD
Daily gain ($kg.d^{-1}$)	2	5.81	2	5.52	3	5.80	1	5.56	1	6.43	2	5.62	1	5.76
Food conversion ratio	2	0.232	2	0.238	3	0.233	0	0.234	0	0.274	2	0.218	0	0.236
Backfat thickness (mm)	1	2.50	1	2.84	1	2.76	1	2.50	3	2.96	1	2.39	2	1.99
Lean parts (%)	1	2.99	1	2.87	1	2.48	1	1.56	1	2.02	1	2.62	1	2.09
Fatty parts (%)	1	2.78	1	2.77	1	2.55	1	1.31	1	1.63	1	2.59	1	2.01
Lean tissue gr. ($kg.d^{-1}$)	2	3.85	1	4.06	2	3.46	1	3.15	1	4.15	1	4.23	1	3.97
Fatty tissue gr. ($kg.d^{-1}$)	1	2.19	1	2.14	1	2.35	1	1.38	1	1.14	1	2.24	1	1.92
Lean tissue food conv.	2	0.866	1	0.956	3	0.762	1	0.535	1	0.737	0	0.807	0	0.697

[1] For DG, LTGR and FTGR (RSD * 10^2).

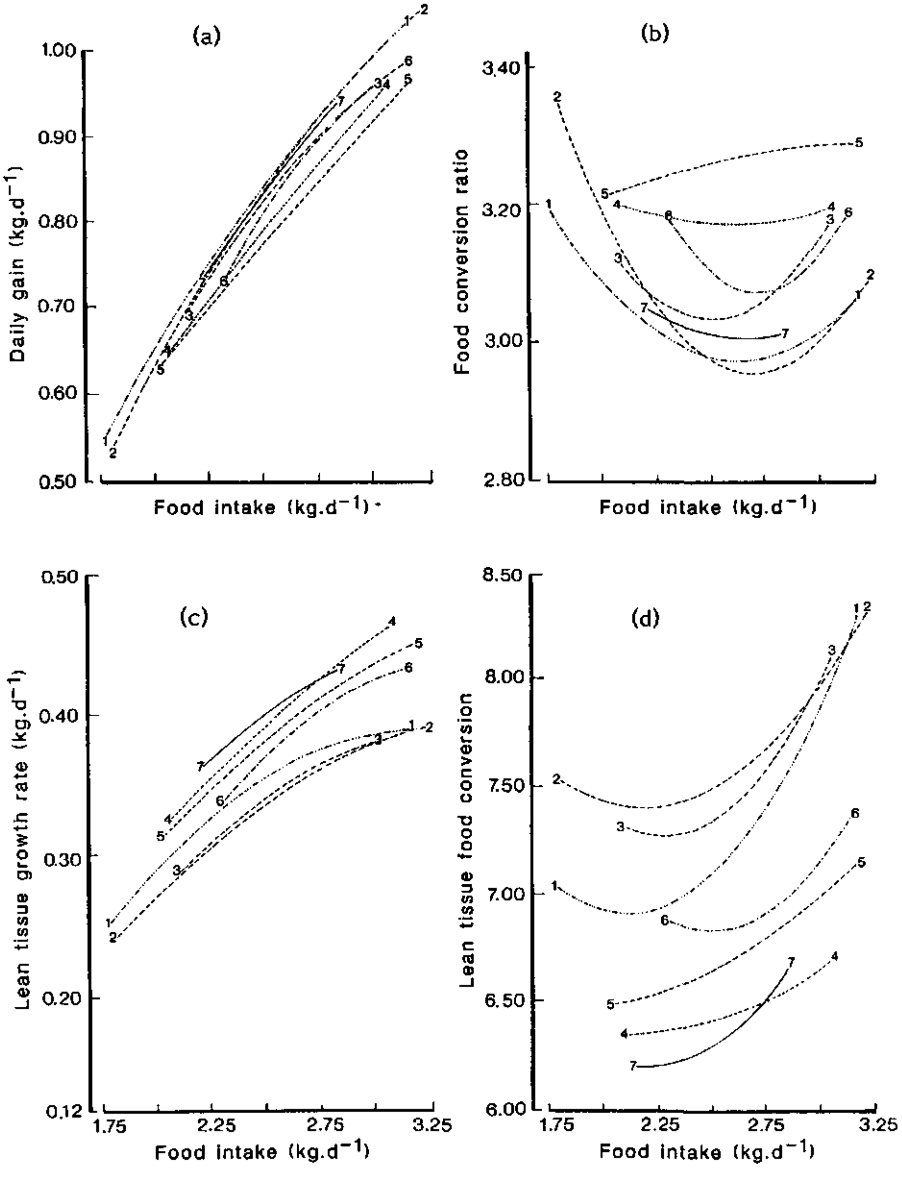

Figure 1. Plots of daily gain (a), food conversion ratio (b), lean tissue growth rate (c) and lean tissue food conversion ratio (d) against average daily food intake, based on quadratic polynomials. Numbers correspond to batches.

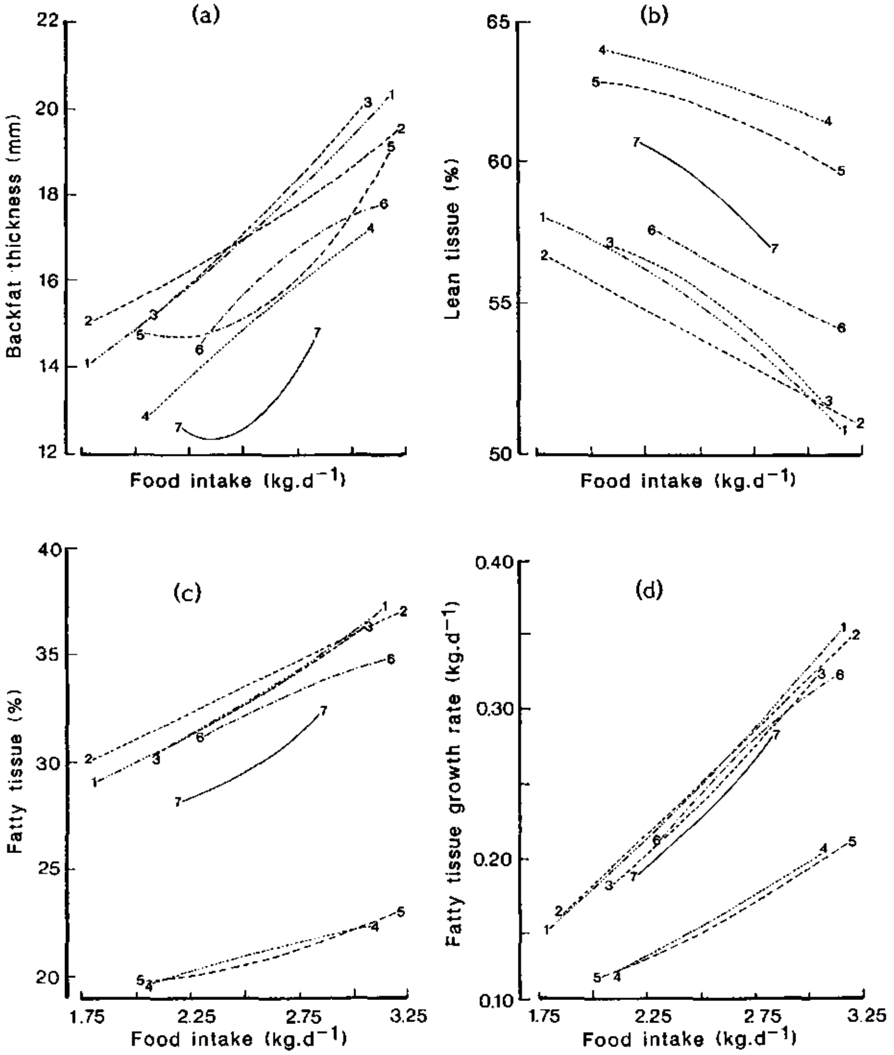

Figure 2. Plots of backfat thickness (a), percentage lean tissue (b), percentage fatty tissue (c) and fatty tissue growth rate (d) against average daily food intake, based on quadratic polynomials. Numbers correspond to batches.

estimates from model 1 and RSD values are presented for DG and LTGR. Parameter estimates from model 2, for FCR and LTFC were similar to those in Table 5 and, therefore, not given here.

Table 5. Parameters and residual standard deviations (RSD*10) for non-linear regression of daily gain and of lean tissue growth rate on average daily food intake ($kg.d^{-1}$) by model 1: $y = a(FI-f_0)^b$.

		Batch						
		1	2	3	4	5	6	7
Daily gain	a	0.720	0.784	0.867	0.517	0.346	0.933	0.530
($kg.d^{-1}$)	f_0	1.169	1.357	1.642	0.697	0.087	1.907	0.670
	b	0.528	0.470	0.321	0.719	0.913	0.271	0.741
	RSD	0.583	0.548	0.592	0.557	0.648	0.566	0.583
Lean tissue	a	0.356	0.331	0.371	0.345	0.328	0.426	0.416
growth rate	f_0	1.558	1.436	1.833	1.171	1.098	2.073	1.660
($kg.d^{-1}$)	b	0.217	0.309	0.187	0.453	0.435	0.155	0.222
	RSD	0.387	0.400	0.346	0.316	0.412	0.424	0.400

Parameters were quite variable over batches and highly correlated. Exponents in Table 5 were between 0 and 1, which means that weight gain and lean tissue gain increased less with increasing FI. The degree of curvature shown by the exponents corresponded well to Figures 1a and 1c. The high b value for batch 5 may be due to the absence of overlap between the food intake data of the two feeding levels. The parameter f_0 may be considered as an estimate of maintenance requirement and seems to be somewhat higher than 1 kg food per day on average. It has a large standard error because its value is outside the range of the data. The coefficient a represents the expected gain at FI equal to f_0+1 $kg.d^{-1}$. Parameters f_0 and b can be estimated with the models 1 and 2 and determine FI at minimum food conversions. In Table 6, these calculated FIs are given for models 2 and 1, and for quadratic polynomials. FI of about 2.6 $kg.d^{-1}$ gave minimum FCR, but this figure is quite variable over batches, although far less variable than f_0 and b. As indicated in the appendix, model 2 allows a very slow increase in FCR at increasing FI. The minimum

LTFC occurred at FI of about 2.2 kg.d^{-1}. Comparing batches 6 and 7, it can be seen that gilts and barrows had a minimum FCR at about the same FI, but that minimum LTFC in gilts was at about 0.25 kg.d^{-1} less than in barrows. Differences between the three approaches were small, with a tendency for the quadratic polynomials to estimate minimal conversion ratios at a somewhat higher FI. Besides, because of the symmetry around the minimum, the quadratic polynomials seem to overestimate conversion ratios at high FI compared with models 1 and 2.

Table 6. Food intake (kg.d^{-1}) giving minimum food conversion ratio and minimum lean tissue food conversion, estimated directly with model 2 (I), indirectly via daily gain and lean tissue growth rate with model 1 (II) and via quadratic polynomials (III).

		Batch						
		1	2	3	4	5	6	7
Food conversion ratio	I	2.489	2.706	2.408	2.501	1)	2.621	2.635
	II	2.477	2.561	2.418	2.481	0.992	2.614	2.586
	III	2.634	2.705	2.509	2.606	1)	2.719	2.656
Lean tissue food conversion ratio	I	1.995	2.068	2.246	2.157	1.777	2.466	2.248
	II	1.990	2.078	2.254	2.140	1.942	2.453	2.133
	III	2.107	2.187	2.276	2.069	1.807	2.492	2.204

1) Not a minimum

The response of BF, LP, FP and FTGR on FI in most batches did not deviate significantly from linear and the curves in Figure 2 showed no consistent curvature. Therefore, in Table 7, parameters and RSD values from the linear regression models are given. The regression coefficients for LP and FP were almost opposite, showing the strong negative correlation between these traits. In batches 4 and 5, the b values for LP, FP and FTGR were closer to zero than in the other batches because of the different dissection technique. The RSD's for FTGR were relatively low, indicating the strong correlation between FTGR and FI.

Table 7. Intercepts (a), regression coefficients (b) and residual standard deviations (RSD) from linear regression of backfat thickness, lean parts, fatty parts and fatty tissue growth rate on food intake ($kg.d^{-1}$).

		Batch						
		1	2	3	4	5	6	7
Backfat thickness (mm)	a	5.95	9.26	4.67	4.32	7.29	6.17	4.21
	b	4.48	3.14	5.02	4.19	3.47	3.77	3.52
	RSD	2.50	2.84	2.76	2.50	3.07	2.39	2.04
Lean parts (%)	a	68.18	64.17	68.88	69.36	69.09	66.98	74.74
	b	-5.35	-4.08	-5.42	-2.52	-2.93	-4.02	-6.18
	RSD	2.99	2.87	2.48	1.56	2.02	2.62	2.09
Fatty parts (%)	a	17.89	21.35	18.04	14.14	14.03	21.44	13.75
	b	6.03	4.87	5.84	2.67	2.72	4.27	6.42
	RSD	2.78	2.77	2.55	1.31	1.63	2.59	2.01
Fatty tissue growth rate ($kg.d^{-1}$)	a	-0.129	-0.109	-0.141	-0.060	-0.053	-0.104	-0.153
	b	0.153	0.144	0.151	0.085	0.081	0.138	0.153
	RSD1)	2.19	2.14	2.35	1.38	1.14	2.24	1.92

1) RSD * 10^2

DISCUSSION

Weight gain and food conversion

The aim of this study was to investigate the response of production traits to increasing FI at high average intake levels. The results should be valid for the whole range of FI expected under practical conditions. The present data differed from many others in that within each feeding level considerable variation existed in actual FI. This intra-feeding-level variation, in combination with variation between feeding levels, gave continuous data points over a wide range of FI (1.7 to 3.2 $kg.d^{-1}$, about 22 to 42 MJ $DE.d^{-1}$).

As expected, the effect of FI on DG was highly significant. Contrary to the conclusion of ARC (1981), which was based on similarity of regressions at different feeding levels in different experiments, the relation may well deviate significantly from linearity. The range in FI in the ARC review was from about 15 to 35 MJ DE.d^{-1}, thus equally long as in the present study but at a lower average. However, the deviation from linearity was not large and on shorter food-intake ranges a linear response may be an acceptable assumption. The average linear regression coefficient in the present experiments with barrows was not much different from the average given in the review by ARC (1981): 23 v. 25 g increase per day for each MJ increase in daily intake of DE. The regression coefficient in gilts was not clearly different from that in barrows, a finding similar to ARC (1981).

The relation between FCR and FI could be described entirely by the relation between DG and FI. Table 4 shows that a change of DG of the 'diminishing-returns type', results in a curvilinear FCR, whereas a linear increase of DG results in a constant FCR. The formula for the minimum FCR shows that, if exponent b in model 1 equals unity, no minimum FCR exists. Figure 1b suggests a rather large effect of FI on FCR in some batches. This is misleading, however, because parameter estimates were inaccurate, as reflected by high RSD values. The effect of FI on FCR in the present experiment was less than in the work of Vanschoubroek et al. (1967), who found a difference of more than 6% between FCR at ad libitum FI and at 75% of ad libitum, but in line with newer concepts of growth and food intake. However, Campbell et al. (1985) found rather strong relations between FCR and energy intake with a minimum FCR at 33 MJ DE per day. This was about 79% and 84% of ad libitum FI for males and females respectively, but these results were based on only 20 animals per sex, grown over a short weight interval. As far as a minimum FCR was found in the present study this occurred at a relatively high level of FI: for barrows about 87% of ad libitum intake and for gilts it was ad libitum.

Body composition and lean tissue gain

Carcasses were not dissected anatomically. However, the correlation between dissection method 1 and the percentage muscle tissue is about 0.95 (P. Walstra, personal communication). Also Metz et al. (1984) showed that the defined LP and FP reflect muscle percentage and adipose tissue percentage almost completely.

On average, 1 kg of extra food intake per day resulted in 4 mm extra backfat (ultrasonically measured), 5% less lean tissue and 5.5% extra fatty tissue (dissection method 1). Comparing batches 6 and 7 at equal FI, gilts had less fat and more lean than barrows, but the regression coefficients showed more response on increasing FI for gilts than for barrows.

From Table 4 it may be concluded that even in barrows at high feeding levels and slaughtered at 108 kg on average, a plateau in LTGR can often not be demonstrated. Figure 1c shows, however, that the linear/plateau model might still hold, but that the plateau for most pigs in the present experiment lies beyond the upper limits of appetite, as also suggested by Campbell et al. (1985) for pigs of 40 kg live weight. An explanation for the fact that a clear plateau could not be found, may be based on the definition of traits. Possibly a plateau for LTGR can be expected only for the last part of the growing period. In that case the chance to find a plateau in the present data was diminished, although, compared to most literature, the average slaughter weight was high. A more definitive way to test the linear/plateau theory would be to relate LTGR to FI, when each is calculated over relatively short parts of the growing period. The most likely result is that a plateau will be found only for the later parts of the growing period.

The linear model for LTGR was also supported by the linear course of FTGR (Table 4, Figure 2d). Should the linear/plateau model hold for LTGR, an increase in FTGR could be expected above the FI where the plateau occurred. Only a non-significant tendency for increasing FTGR was found. The linear correlation between FTGR and FI was so high it leads to the conclusion that, in the range of FI studied, an almost fixed part of the food for production was used for deposition of fatty tissue.

Lean tissue food conversion

In batches 1 to 5, a significant effect of FI on LTFC was found (Table 4). RSD values of the models were high, however, and the effect was not consistent. In batches 6 and 7, no significant effect was found, which may be associated with the shorter range of food intake and with the deviating feeding scheme. Also the curves given by ARC (1981) did not indicate much effect of food intake level on LTFC. Based on the diminishing-returns concept for LTGR, a curvilinear relation for LTFC is plausible. Gilts had a better LTFC than barrows (Table 3 and Figure 1d) and a minimum at a lower FI (Table 6). Relative to the average ad libitum FI in batches 6 and 7, each sex had its optimum LTFC at about 86% of ad libitum FI. Because of the short range of FI in batches 6 and 7, however, this value is not reliable and results for the other batches indicated that for barrows an optimum LTFC at about 75% of ad libitum intake is more likely.

The quadratic polynomials and the non-linear models tended towards higher LTFC at higher FI and an optimal FI at about 2.2 $kg.d^{-1}$, being as much as 0.4 $kg.d^{-1}$ lower than with respect to FCR. The main reason for reaching the minimum LTFC at a lower FI than the minimum FCR was the stronger diminishing-returns type form of the LTGR response curve compared with the DG response curve. This was clearly demonstrated by the lower b values for LTGR (Table 5), which were not fully compensated for by the slightly higher f_0 values. The different degrees of bending in the curves for DG and LTGR were caused mainly by FTGR, which already increased faster than LTGR at moderate feeding levels. Therefore, the response of DG to increasing FI approximated a straight line more than the response of LTGR alone.

These results indicate that the optimum feeding level, from an economical viewpoint, depends much on the way carcasses are classified and paid. If the price of a carcass is influenced heavily by the percentage lean, then the optimum feeding level is lower than if the percentage lean plays only a minor role. Moreover, if by genetic or environmental changes the diminishing-returns character of the LTGR curve can be reduced, then the optimum feeding level will increase.

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APPENDIX

The following non-linear model was fitted to DG and LTGR as an alternative to quadratic polynomials:

$$y = a(FI-f_0)^b \qquad \text{(model 1)}$$

The corresponding model for FCR and LTFC was:

$$y = \frac{FI}{a(FI-f_0)^b} \qquad \text{(model 2)}$$

As an example, both models are shown in Figure 3 for DG and FCR in batch 2.

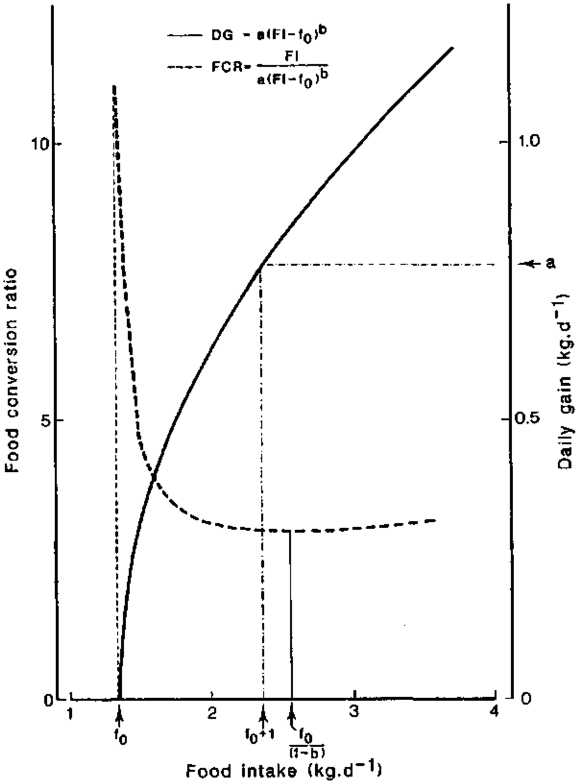

Figure 3. Schematic representation of model 1 and model 2 for daily gain (DG) and food conversion ratio (FCR), respectively.

The parameter f_0 is the FI at zero DG and can, in that case, be considered as a maintenance requirement. However, due to the relatively strong regression at DG close to zero, f_0 is probably an overestimate of maintenance requirement. The parameter a can be considered as the DG or LTGR if FI is 1 $kg.d^{-1}$ above f_0. If the parameter b equals 1, the relation is exactly linear, whereas $0<b<1$ or $b>1$ represent relations of the diminishing- or increasing-returns type, respectively.

Model 2 has the same parameters as model 1. An advantage of model 2, compared with a quadratic polynomial, is that it is not necessarily symmetric around the minimum at $FI=f_0/(1-b)$. This allows a slight increase in FCR after the minimum at increasing FI, which is biologically acceptable.

CHAPTER 2

EFFECT OF FOOD INTAKE CAPACITY ON PRODUCTION TRAITS IN GROWING PIGS WITH RESTRICTED FEEDING

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ABSTRACT

Food intake capacity (FIC), defined as average daily voluntary food intake during a growing period from about 27 to 107 kg live weight, was estimated in 438 pigs in seven batches, fed at restricted feeding levels. Batches 1 to 6 consisted of barrows and batch 7 of gilts. Animals fed at a restricted feeding level had one to three ad libitum fed littermates. In batches 6 and 7, animals fed 'restrictedly' were fed ad libitum to 48 kg live weight and according to scale afterwards.

The first method of estimating FIC was applied in each batch and consisted of assigning the average daily food intake (FI) of ad libitum fed littermates to each animal fed at a restricted feeding level. The second method was applied to batches 6 and 7 only and consisted of estimating FIC with multiple regression based on individual 'ad libitum performance' in the first part of the growing period.

Effects of FI and FIC on daily gain, food conversion ratio, backfat thickness, percentage lean parts, percentage fatty parts, lean tissue growth rate, fatty tissue growth rate and lean tissue food conversion were investigated. FI had a significant effect on each trait, except on lean tissue food conversion. FIC had a significant effect on body composition traits, but not on daily gain and food conversion ratio.

Irrespective of the method used to estimate FIC, results showed that animals with a higher FIC produced more fat and less lean from the same amount of food than animals with a lower FIC. It was suggested that the partition of metabolizable energy between energy for maintenance, protein deposition and fat deposition is associated with FIC. The findings confirmed that selection for leaner and more efficient pigs may result in animals with lower FIC, irrespective of the feeding regimen during performance testing.

INTRODUCTION

Comparisons between breeds or lines generally show that leaner types of pigs eat less food per day, on average, than fatter types (King et al., 1975; Cöp and Buiting, 1977; Brascamp, 1981; Henry, 1983). Genetic correlations between ad libitum food intake and percentage meat in the carcass are generally negative (Swiger et al., 1979; Waefler et al., 1983).

When feeding is ad libitum, leaner types of animals are lean because their average daily food intake (FI) is lower. As a consequence, less energy is available for fat accretion. In other words, leaner types of animals restrict themselves in FI. Thus, partition of food energy above maintenance requirement between lean tissue and fatty tissue depends on the amount of food. With ad libitum feeding, however, the actual FI is confounded with (voluntary) food intake capacity (FIC). Therefore, partition of food energy may also depend on FIC, apart from actual FI. In this case, two animals eating the same (restricted) amount of food, but each animal having a different FIC, would have a different partition of that food energy and so would have a different body composition at slaughter.

In this paper, FIC is defined as the average daily ad libitum or voluntary food intake over the total growing period. FIC can only be measured when animals are fed ad libitum, but then effects of FI and FIC are completely confounded. A possibility to overcome this is to feed animals at a restricted feeding level and to estimate their FIC. The aim of this paper is to study whether estimated FIC in animals fed restrictedly has an effect on production traits, in addition to the effect of actual FI. Two methods of estimating FIC will be applied. Effects will be discussed with special reference to consequences for selection.

MATERIAL AND METHODS

Animals and feeding

Results of 438 growing pigs fed at restricted feeding levels were available for this study. Animals were Dutch Yorkshire * Dutch Landrace crossbreds, individually housed and fed (hand feeding of pellets twice a day). Pigs were fattened in six experiments from 1976 to 1982 at the Agricultural University experimental station De Haar. Animals in experiments 1 to 5 were barrows, whereas those in experiment 6 were barrows and gilts from the same litters. Each experiment was considered as one batch, except experiment 6 where barrows and gilts were considered as two separate batches.

In each of the seven batches, up to three animals per litter were fed ad libitum and two or three were fed restrictedly on different feeding levels. Number of litters per batch and assignment of animals to feeding levels is given by Kanis (1988). In batches 1, 2 and 3, restrictedly fed animals received a fixed proportion (batches 1 and 2: 0.85, 0.74 or 0.65; batch 3: 0.85

or 0.74) of the food eaten by one randomly chosen ad libitum fed littermate (reference animal) at the same live weight. In batches 4 and 5, litters were paired at random. In each litter of a pair animals fed at a restricted feeding level received food according to the average ad libitum food intake of two randomly chosen reference animals in one litter of that pair (the reference litter, whereas the other litter was the linked litter). Restricted feeding levels were 0.80 (batch 4) and 0.74 (batch 5) of ad libitum. In batches 6 and 7, animals were fed ad libitum from 27 till 48 kg live weight. After this weight, in each batch 67 animals were switched to restricted feeding according to a fixed scale (0.85 or 0.74 of the average ad libitum intake in previous batches).

Animals were weighed individually and food intake was recorded weekly. The amount of food intended for each animal fed at a restricted level was calculated on the basis of its own live-weight gain and the ad libitum food intake of its reference animal(s) at similar weight(s). The food in batches 1 to 4 contained 13.03 MJ digestible energy (DE) and 162 g crude protein (CP) per kg. In batches 5 to 7 the food contained 13.41 MJ DE and 172 g CP per kg. To correct for the small difference between batches in energy content of the food, food intake in batches 5 to 7 was multiplied by 1.029. At the end of the growing period, backfat thickness was measured ultrasonically, and animals were slaughtered and dissected into lean and fatty parts. The composition of the food mixture by batch, as well as the dissection methods, are described by Kanis (1988).

Estimation of food intake capacity

FIC was estimated by two methods. The first method (method 1) was applied to all animals fed at a restricted feeding level. It consisted of assigning to each animal fed restrictedly, the mean of the average daily food intake(s) of its ad libitum fed littermate(s) of the same sex (FIC_l; l=littermate). This means that FIC_l in batches 1, 2, 3, 6 and 7 was based on one littermate and in batches 4 and 5 on two or three littermates. With this method, animals in one litter received the same value for FIC_l. The accuracy of estimating FIC_l depends, among others, on the number of ad libitum fed animals in a litter (see Appendix).

The second method of estimating FIC (method 2) was applied only to batches 6 and 7 because it was based on individual performance in the first part of the growing period (about 27 to about 48 kg live weight), when feeding was ad libitum (FIC_p; p=performance). Cumulative ad libitum food intake and number of days in the second part of the growing period, when feeding was restricted, were predicted by separate multiple regression equations developed for ad libitum fed animals of each sex. Traits recorded during the first period, giving lowest residual standard deviation for the second period, were: live weight and age at the start of the growing period, actual weight gain, number of days and cumulative food intake from 27 to 48 kg live weight, and actual weight gain from 48 kg to slaughter weight. (Slaughter weight was considered as a management factor and known beforehand). FIC_p in animals fed restrictedly was estimated as:

$$FIC_p = \frac{\text{food intake period 1 + estimated food intake period 2}}{\text{days period 1 + estimated days period 2}} .$$

Effects of estimated FIC

Effects of actual food intake and estimated food intake capacity on production traits were investigated using the statistical model (Harvey, 1977):

$$y_{ij} = \mu + g_i + b_1(X_{1ij} - \bar{X}_1) + b_2(X_{2ij} - \bar{X}_2) + e_{ij} \qquad \text{(model 1)}$$

where

y_{ij} = production trait of animal j in batch i
μ = general mean
g_i = effect of batch i (i=1 to 7, or i=6,7)
X_{1ij} = actual food intake (FI in $kg.d^{-1}$)
X_{2ij} = estimated food intake capacity (FIC_1 or FIC_p in $kg.d^{-1}$)
$\bar{X}_1$ = mean food intake ($kg.d^{-1}$)
$\bar{X}_2$ = mean food intake capacity ($kg.d^{-1}$)
b_1, b_2 = partial regression coefficients
e_{ij} = random error.

Tests of equality of regression coefficients within batches were carried out with a similar model including regression within batches.

In the Appendix it is shown that the magnitude of the partial regression coefficient b_2 in model 1 depends on the variance of X_{2ij}. The value of b_2 increases with increasing accuracy of estimation of FIC_1, but decreases with increasing accuracy of estimation of FIC_p.

RESULTS

Average food intake and production traits

The number of animals in each batch and food intake characteristics are presented in Table 1. Because of treatment differences between batches, batch averages should not be compared, except batches 6 and 7 where barrows and gilts from the same litters were kept under similar conditions. The feeding level of restrictedly fed animals in batches 6 and 7 was relatively high because of ad libitum feeding in the first part of the growing period and because of the relatively low ad libitum intake, especially for gilts.

Table 1. Number of animals, means ($\bar{x}$) and standard deviations (s) for food intake characteristics.

		Batch						
		1	2	3	4	5	6	7
Ad libitum feeding								
No. of animals		25	25	20	100	46	33	33
Food intake ($kg.d^{-1}$)	$\bar{x}$	2.933	3.001	2.941	2.819	2.925	2.919	2.613
	s	0.241	0.215	0.106	0.254	0.249	0.226	0.219
Restricted feeding								
No. of animals		74	74	33	96	39	61	61
Food intake ($kg.d^{-1}$)	$\bar{x}$	2.169	2.237	2.352	2.200	2.125	2.451	2.389
	s	0.283	0.302	0.192	0.146	0.113	0.142	0.140
Feeding level (%)1)	$\bar{x}$	73.97	74.62	80.12	78.60	72.79	84.72	92.10
	s	8.63	8.53	6.08	7.01	4.66	8.11	8.50

1) Actual average daily food intake, divided by the mean of the average intake(s) of ad libitum fed littermates of the same sex, multiplied by 100%.

Production traits of animals fed at a restricted levels are in Table 2. Percentages of lean parts and fatty parts in batches 4 and 5 deviated from those in other batches, mainly because of different dissection methods. Although the values in Table 2 do not include ad libitum fed animals, average daily gain was higher than average results from Dutch fattening practice (Consulentschap in Algemene Dienst voor Varkenshouderij, 1985).

Table 2. Means ($\bar{x}$) and standard deviations (s) for production traits of animals fed at restricted feeding levels.

		Batch						
		1	2	3	4	5	6	7
Daily gain ($kg.d^{-1}$)	$\bar{x}$	0.714	0.732	0.778	0.694	0.671	0.783	0.787
	s	0.126	0.140	0.086	0.071	0.071	0.073	0.072
Food conversion ratio	$\bar{x}$	3.066	3.098	3.041	3.188	3.193	3.144	3.055
	s	0.252	0.297	0.196	0.251	0.284	0.219	0.245
Backfat thickness (mm)	$\bar{x}$	15.60	16.16	16.73	13.88	14.60	15.47	12.61
	s	2.81	2.87	2.53	2.74	2.83	2.29	2.01
Lean parts (%)	$\bar{x}$	56.57	55.08	55.68	63.52	62.80	57.14	59.91
	s	3.41	3.23	2.45	1.70	2.28	2.47	2.44
Fatty parts (%)	$\bar{x}$	30.96	32.21	32.00	20.18	19.92	31.82	29.09
	s	3.30	3.28	2.74	1.43	1.77	2.44	2.31
Lean tissue growth rate ($kg.d^{-1}$)	$\bar{x}$	0.313	0.305	0.327	0.347	0.332	0.362	0.385
	s	0.052	0.056	0.034	0.035	0.040	0.043	0.042
Fatty tissue growth rate ($kg.d^{-1}$)	$\bar{x}$	0.202	0.213	0.222	0.128	0.121	0.234	0.212
	s	0.047	0.048	0.034	0.019	0.013	0.030	0.028
Lean tissue food conversion	$\bar{x}$	7.020	7.468	7.229	6.385	6.489	6.842	6.278
	s	0.876	0.996	0.608	0.581	0.776	0.753	0.710

Estimation of food intake capacity

The intra-class correlation of ad libitum food intake among littermates (equation 1, Appendix) was 0.291. Therefore, the correlation between expected and estimated FIC_1 is 0.291, 0.362 and 0.401, based on one, two or three ad libitum fed littermates, respectively (equation 2, Appendix).

In the second method, applied to batches 6 and 7, estimation of FIC_p was based on individual performance in the first part of the growing period. In the ad libitum fed animals, coefficients of determination (R^2) for estimating the cumulative food intake in the second part of the growing period were 0.72 (batch 6) and 0.28 (batch 7). For number of days, these values were 0.35 (batch 6) and 0.57 (batch 7). Correlations between FI and estimated FI during the entire growing period for ad libitum fed animals were 0.65 (batch 6), and 0.77 (batch 7). These high values compared with those for FIC_1 were partly the result of part-whole correlations between the first part and the total growing period. In the animals fed at a restricted feeding level, correlations between FI and FIC_p were 0.36 (batch 6), and 0.30 (batch 7).

The two methods estimated FIC quite differently, as illustrated by low correlations between FIC_1 and FIC_p in restrictedly fed animals: 0.12 (batch 6), and 0.27 (batch 7).

Effects of FIC on production traits

Although the magnitude of partial regression coefficients of production traits on FIC_1 depends on accuracy of estimating FIC_1 (see Appendix), within-batch regression coefficients from model 1 were not significantly different between batches for most traits. Therefore, in Table 3 regression coefficients for FI and FIC_1 are presented, pooled over batches.

Table 3. Pooled partial regression coefficients of production traits on FI (b_1) and FIC_1 (b_2), and their F probabilities (P).

	b_1	P	b_2	P
Daily gain ($kg.d^{-1}$)	0.394	0.00	0.002	0.85
Food conversion ratio	-0.321	0.00	-0.005	0.99
Backfat thickness (mm)	3.451	0.00	1.215[1]	0.04
Lean parts (%)	-3.911	0.00	-1.482	0.01
Fatty parts (%)	4.510	0.00	1.522	0.01
Lean tissue growth rate ($kg.d^{-1}$)	0.131	0.00	-0.015	0.08
Fatty tissue growth rate ($kg.d^{-1}$)	0.135[1]	0.00	0.011	0.02
Lean tissue food conversion	0.196	0.31	0.290	0.12

1) Within-batch regression coefficients significantly different ($P<0.05$)

Except for LTFC, partial regression coefficients of production traits on FI were significantly different from zero, indicating the strong effect of FI, even if, as was the case here, only animals fed at a restricted feeding level are considered. For most traits, the sign of the regression on FIC_1 was the same as on FI, but significant differences from zero were only found for body composition traits. Results showed that at the same FI, animals with a higher FIC_1 had more fat and less lean than animals with a lower FIC_1 (Table 3). Pooled regression coefficients of BF, LP and FP on FIC_1 were about 0.35 of the value for FI, which indicated a rather strong influence of FIC_1 on body composition. The within-batch regression coefficients on FIC_1 generally had the same sign as pooled regression coefficients, except for batch 2 and, to a lesser extent, for batch 5 where some were of opposite sign. However, only in batches 4 and 7, within-batch regressions on FIC_1 were significantly different from zero ($P<0.05$).

Partial regression coefficients on FI and FIC_p, pooled over batches 6 and 7, are given in Table 4. To compare both methods of estimating FIC, also pooled partial regressions on FI and FIC_1 are tabulated for these batches. Results for FIC_1 corresponded well to those in Table 3, pooled over all batches. Results for FIC_p tended to the same conclusion as results for FIC_1, although only the partial regression coefficient of FTGR on FIC_p was significantly different from zero ($P<0.05$). For LP, FP and FTGR, partial regression coefficients on FIC_p within batches 6 and 7 were significantly different ($P<0.05$). In gilts, results were more pronounced than in barrows, in showing that a lower FIC yields a leaner pig, irrespective of the actual FI.

DISCUSSION

FIC based on littermates

Inconsistency of regression coefficients between batches indicated that effects of FIC_1 on production traits are hard to demonstrate. One reason for this could be the relatively low correlation of ad libitum food intake between littermates, as expressed in the intra-class correlation (t), and the low numbers of ad libitum fed littermates (n). In batches 1 to 3, t could not be estimated because only one ad libitum fed animal per litter was available. There is no reason, however, to assume that it deviates significantly from 0.29, which was the pooled estimate in the other batches. In fact this value was not lower than the expectation. Theoretically, the expectation of intra-class correlation among littermates is equal to $0.5h^2+c^2$, where h^2 is the heritability and c^2 is the common environment component. Values of $h^2=0.30$ and $c^2=0.15$, as used by Knap et al. (1985), result in $t=0.275$. The value of the regression coefficient b_2 on FIC_1 increases with increasing n (see Appendix). In the present experiment, with $\hat{t} = 0.29$ and a maximum value of 0.40 at $n=3$, b_2 was 0.55 of its theoretical maximum value which is reached at very large n. This indicates that the true effect of FIC may be higher than demonstrated in Table 3. It might be possible to improve the estimate of FIC_1 in animals fed at a restricted level by developing, in the ad libitum fed animals, a multiple regression equation containing not only FI of full sibs but, for example, also DG and BF as independent variables. This has not been done

Table 4. Partial regression coefficients of production traits on FI (b_1) and FIC (b_2), and F probabilities (P), pooled over batches 6 and 7 for both methods of estimating FIC. See text for methods.

	FIC_p				FIC_1			
	b_1	P	b_2	P	b_1	P	b_2	P
Daily gain ($kg.d^{-1}$)	0.330	0.00	0.036	0.17	0.348	0.00	-0.007	0.76
Food conversion ratio	-0.086	0.59	-0.133	0.25	-0.155	0.31	0.029	0.76
Backfat thickness (mm)	3.894 1)	0.01	1.319	0.19	4.362 1)	0.00	0.536	0.52
Lean parts (%)	-4.612	0.00	-1.705 1)	0.14	-4.980	0.00	-1.618	0.09
Fatty parts (%)	4.934	0.00	1.278 1)	0.25	5.019	0.00	1.957	0.03
Lean tissue growth rate ($kg.d^{-1}$)	0.117	0.00	0.008	0.68	0.123	0.00	-0.017	0.27
Fatty tissue growth rate ($kg.d^{-1}$)	0.145	0.00	0.022 1)	0.02	0.149	0.00	0.013	0.10
Lean tissue food conversion	0.377	0.45	-0.125	0.73	0.266	0.34	0.339	0.25

1) Within-batch regression coefficients significantly different ($P<0.05$).

because it was only practicable in batches 4 and 5 where more than one animal per litter and per sex were fed ad libitum.

Another reason for the inconsistent effect of FIC_1 on production traits between batches may be the confounding of actual FI and FIC_1 for the reference litters in batches 1 to 5. Because of direct linkage of restrictedly fed animals to ad libitum fed littermates in these batches, the average correlation between FI and FIC_1 was 0.5 in the reference litters. In the linked litters, this correlation was zero. In batches 6 and 7, the average correlation between FI and FIC_1 was greater than zero (0.16), probably because of the ad libitum intake in the first part of the growing period. To study this effect of confounding, model 1 was also used to analyse a subset of the total data set consisting of 198 animals, which were the linked litters in batches 4 and 5 and animals in batches 6 and 7. In this subset, there was no significant correlation between FI and FIC_1. The pooled and the within-batch partial regression coefficients on FIC_1, as well as their significance levels, were similar to those calculated for the entire data set. This means that confounding of FIC_1 and actual FI was not important for interpretation of results.

FIC based on individual performance

A disadvantage of estimating FIC by method 1 is the necessity of having ad libitum fed sibs. Method 2 was based completely on individual performance in the first part of the growing period. There are several possibilities to predict ad libitum performance in the second part of the growing period from ad libitum performance in the first part. One possibility is to extrapolate growth curves and food intake curves fitted to the data in the first part of the growing period. In the present experiments however, this first part was too short for a sufficient accuracy. The use of average daily food intake and average daily gain in part 1 to predict the same traits in part 2 is another possibility. Correlations between those traits in the two parts, however, were low (on average 0.22 for FI and 0.12 for DG), which agreed with results from Cöp et al. (1970). Cumulative food intakes, weight differences and number of days in the first part were good predictors of cumulative food intake and number of days in the second part. Correlation between actual FI and estimated FIC_p was about 0.7 for 33 ad libitum fed animals of each sex. Extension of the first (ad libitum) period will enlarge this value, but also the degree of confounding with actual FI. The correlation between FI and FIC_p for the animals fed at a restricted feeding level was about 0.33, indicating that the degree of confounding was not high using 27 to 48 kg live weight for the first period. Application of the prediction equations in other animals than in those where they were developed in, as done with the restrictedly fed littermates, may have reduced prediction accuracy. A more general application to non-littermates, kept under different circumstances, may reduce accuracy even further. To study this, FIC_p of ad libitum fed animals in batches 1 to 5 was also estimated with the equations developed in batch 6. Correlations between estimated and actual ad libitum food intake averaged 0.35, ranging from 0.14 to 0.76. This indicates that estimation of FIC, based on individual performance by means of general equations, can be as accurate as estimation based on full-sib information. Variation in accuracy, however, seems to be great, which makes the second method rather risky.

General

Results showed that animals with a higher FIC not only eat more ad libitum and, therefore, deposit more fat, but also produce more fat when they eat the same amount of food as animals with a lower FIC. Comparing two groups of pigs, each having eaten on average the same amount of food per day during the growing period (restrictedly), the group with the highest FIC generally will be the fattest. In other words, the most restricted feeding, relative to FIC, gives the lowest percentage lean parts. This was also suggested by Brascamp et al. (1978), based on the results of the first two batches only. They found, however, that pigs with a higher FIC also had a significantly ($P<0.05$) thinner backfat layer on the carcass. This last result can now be imputed to the somewhat deviant values in batch 2, which were also found for ultrasonic backfat thickness in the present study.

Partial regression coefficients of body composition traits on FIC_l and on FIC_p were about 0.35 those on FI. No significant effects of FIC on DG and FCR were found. It seems, therefore, that FIC is associated with the ratio in which the consumed metabolizable energy is partitioned between energy for maintenance, for protein deposition and for fat deposition. Apparently, animals with lower FIC spend relatively more energy on lean growth and less on fat growth. At equal FI, however, their total growth rate is not higher. Assuming that energy needed per unit of deposited lean and of fat does not differ between animals with high and low FIC, leaner types of animals with lower FIC would have higher maintenance requirement. Higher maintenance requirement for leaner pigs has been suggested by several authors, e.g. Sundstøl et al. (1979); Wenk et al. (1980); Whittemore (1983).

For breeding, boars and gilts are more relevant than barrows. It is not clear that the demonstrated effects of FIC also hold for boars, which normally have a lower potential for food intake and fat production. However, in gilts, which for these traits are more or less intermediate between boars and barrows, the effect of FIC was similar to that in barrows. The results agree with recent research concerning selection for production traits, in which it is often stated that selection for leaner and more efficient pigs may easily result in pigs with a lower FIC (Fowler et al., 1976; Smith and Fowler, 1978; Kalm and Krieter, 1985; Webb and Curran, 1986). This is true, not only for testing with ad libitum feeding, but also with restricted feeding. In the latter case, this may be even more serious because FIC can not be observed. In the long term, a continuing decrease of FIC is not desired because it may limit the improvement of average daily gain. However, increasing the FIC by selection, without sufficient attention to LTGR, may result in fatter pigs, even if the actual amount of food given to the pigs is not increased. Further studies on optimizing selection for production traits and food intake in the long term are still necessary.

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APPENDIX

Accuracy of estimating FIC

Accuracy of estimating FIC_1 was assessed by the intra-class correlation (t) for food intake among ad libitum fed littermates, using analysis of variance (Harvey, 1977). Data to estimate the intra-class correlation contained ad libitum fed animals in experiments 4, 5 and 6. Because animals in experiment 6 consisted of barrows and gilts from the same litters on the same treatments, ad libitum food intake of gilts was first corrected for effect of sex by increasing it with 0.307 $kg.d^{-1}$. This was the average difference between barrows and gilts after correction for litter effects. The model used to estimate t was:

$$y_{ijk} = \mu + G_i + L_{j:i} + e_{ijk}$$

where

y_{ijk} = ad libitum food intake of animal k from litter j within experiment i

μ = general mean

G_i = fixed effect of experiment i (i=4, 5 or 6)

$L_{j:i}$ = random effect of litter j within experiment i

e_{ijk} = random error.

The intra-class correlation t was estimated as:

$$\hat{t} = \frac{\hat{\sigma}_L^2}{\hat{\sigma}_L^2 + \hat{\sigma}_e^2} \qquad (1)$$

where $\hat{\sigma}_L^2$ and $\hat{\sigma}_e^2$ are estimated components of variance for litter effects and error.

The intra-class correlation can be considered as accuracy of predicting FIC_1 based on one ad libitum fed littermate. When FIC_1 is estimated as average of n littermates, this accuracy can be estimated as:

$$\hat{t}_n = \sqrt{\frac{n * \hat{t}^2}{1 + (n - 1)\hat{t}}} \qquad (2)$$

The accuracy of estimating FIC_p was evaluated by the correlation between actual FI and FIC_p for the ad libitum fed animals in batch 6 and 7.

Effect of accuracy of estimating FIC on b_2

To calculate the ratio of actual and true partial regression coefficients ($b_{2\ act.}/b_{2\ true}$) suppose that:

y = production trait at fixed restricted FI within batch
FIC_e = estimated food intake capacity (FIC_1 or FIC_p)
FIC_t = true food intake capacity
r_g = genetic correlation between y and FIC_t
r_p = phenotypic correlation between y and FIC_t
r = correlation between FIC_e and FIC_t
h_y = positive square root of heritability for y
h_{FIC_t} = positive square root of heritability for FIC_t.

For method 1 (FIC_1), the following relationship can be derived:

$$b_{2\ act.} = b_{y,FIC_e} = \frac{cov(y,FIC_e)}{var\ FIC_e} = \frac{cov(y,FIC_{full\ sib})}{\frac{1+(n-1)t}{n}\sigma^2_{FIC_t}}.$$

Assume:

$$cov(y,FIC_{full\ sib}) = 0.5\ r_g\ h_y\ h_{FIC_t}\ \sigma_y\ \sigma_{FIC_t}$$

and

$$b_{2\ true} = b_{y,FIC_t} = \frac{cov(y,FIC_t)}{var\ FIC_t} = \frac{r_p\ \sigma_y\ \sigma_{FIC_t}}{\sigma^2_{FIC_t}} = r_p\frac{\sigma_y}{\sigma_{FIC_t}},$$

then

$$\frac{b_{2\ act.}}{b_{2\ true}} = \frac{0.5\ r_g\ h_y\ h_{FIC_t}}{r_p} * \frac{n}{1+(n-1)t} = C * \frac{n}{1+(n-1)t},$$

where C is a constant.

Thus, the actual partial regression coefficient of production traits on FIC_1 appears to increase with increasing n.

For method 2 (FIC_p), assume:

$FIC_t = FIC_e + \underline{e}$ where $\underline{e}$ = random error,

$\text{var } FIC_t = \text{var } FIC_e + \text{var } \underline{e}$

$\text{cov}(y,FIC_t) = \text{cov}(y,FIC_e + \underline{e}) = \text{cov}(y,FIC_e)$

$$b_{2\text{ act.}} = b_{y,FIC_e} = \frac{\text{cov}(y,FIC_e)}{\text{var } FIC_e}$$

$$b_{2\text{ true}} = b_{y,FIC_t} = \frac{\text{cov}(y,FIC_t)}{\text{var } FIC_t} = \frac{\text{cov}(y,FIC_e)}{\text{var } FIC_t}$$

$$\frac{b_{2\text{ act.}}}{b_{2\text{ true}}} = \frac{\text{var } FIC_t}{\text{var } FIC_e} = \frac{1}{r^2}$$

Thus for FIC_p, the actual partial regression coefficient decreases with increasing accuracy of estimation.

CHAPTER 3

EFFECT OF FOOD INTAKE CAPACITY ON GENOTYPE BY FEEDING REGIMEN INTERACTIONS IN GROWING PIGS

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Submitted for publication to Animal Production.
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ABSTRACT

From each of 130 litters, one to three pigs were fed ad libitum and one to four were fed at several restricted feeding levels from about 27 to 107 kg live weight. Six experiments were combined to three groups. In group A (barrows), animals fed at a restricted feeding level received a proportion of their estimated food intake capacity (FIC). In group B (barrows), litters were joined two and two to pairs. Animals fed at a restricted level in the first litter of each pair were fed according to FIC, whereas in the other litter an amount equal to that of the first litter was given to restrictedly fed animals, irrespective of FIC. Group C consisted of barrows and gilts that were fed ad libitum to 48 kg live weight. Thereafter two-third of the animals were fed according to scale.

Litter by feeding regimen (ad libitum v. restricted feeding) interactions (L*F) were significant in group B for daily food intake (FI), daily gain, lean tissue growth rate and fatty tissue growth rate. In group C, sex by feeding regimen interactions (S*F) were significant for the same traits. Significant L*F or S*F interactions were not found for body composition and food conversion traits.

Absence of significant interactions in group A indicated that interactions in groups B and C were probably related to variation in degree of food intake restriction (DFR). In groups B and C, correction of FI and production traits of restrictedly fed animals for differences in DFR, resulted in disappearance of L*F and S*F interactions. It was concluded, therefore, that the poor relationships often found between test-station results of boars and results of their progeny in practical environments may be caused, to a large extent, by differences in DFR in each environment. The easiest way to prevent these genotype by environment interactions is to feed animals ad libitum in test and commercial environments.

INTRODUCTION

In most pig-breeding programmes, genetic response to selection for production traits is based mainly on central tests in standardized environments. The breeding goal, however, is generally defined for commercial conditions that may be very variable (Brascamp et al., 1985). A starting point of all breeding programmes is the assumption that the best genotypes in central-test environments will produce the best progeny in commercial environments. In cases of genotype by environment interaction (GEI), however, this is not necessarily true.

Existence of GEI in pig-breeding programmes has often been shown (e.g. Ketelaars, 1979; Claus et al., 1984; Busse and Groeneveld, 1986). GEI arises most frequently and most seriously in traits such as daily gain and food conversion, and not often in body composition traits (King, 1972; Ollivier et al., 1984; Steane et al., 1984). The feeding regimen, e.g. ad libitum or restricted feeding, seems to be one of the major environmental factors in GEI (King, 1972; Kempster, 1974; Ollivier et al., 1984; Steane et al., 1984; Webb and Curran, 1986). It is well known that under commercial conditions a large variety of feeding regimens can be found, ranging from ad libitum via semi-ad libitum to feeding according to weight or age. But also in test-stations the feeding regimen is less standardized than one would expect. Ad libitum feeding allows between animal variation in daily food intake, and this can be considerable (Wyllie et al., 1979; Kanis, 1988a). Normal scale feeding, however, does not account for food intake capacity (FIC; defined as average daily ad libitum food intake over the total growing period). Thus animals receiving the same amount of food according to weight or age, may be restricted to different degrees. Kanis (1988b) showed that FIC, corrected for differences in actual (restricted) food intake, had a significant influence on body composition. Pigs with a higher estimated FIC produced more fat and less lean from the same (restricted) amount of food than pigs with a lower estimated FIC.

A special form of GEI is sex by feeding regimen interaction (S*F). Because of well known differences in FIC between sexes, S*F interaction may occur when sexes are compared on ad libitum and restricted feeding (Walstra et al., 1977; Campbell and King, 1982). Donker et al. (1986) suggested that S*F interactions are absent if food restriction is related to FIC. In a breeding programme, S*F interactions can be important if breeding values are only based on information from one sex.

The aim of this paper is to investigate how important differences in FIC or in degree of food intake restriction are for genotype by feeding regimen and for sex by feeding regimen interactions. Implications for breeding programmes will be discussed.

MATERIAL AND METHODS

Animals and feeding

Data from pigs fattened in six experiments (exp. 1 to 6) were used. Experiments with similar experimental designs (Table 1) were grouped. Group A consisted of animals from exp. 1, 2 and 3, containing 25, 25 and 20 litters, respectively. Exp. 1 and 2 had four barrows per litter each, of which one was fed ad libitum and the others restrictedly on 85%, 74% or 65% of the intake of the ad libitum fed littermate at the same live weight. In exp. 3, a similar design was chosen except the 65% feeding level was omitted. Group B consisted of animals from exp. 4 and 5, containing 40 and 16 litters with five or six barrows per litter, respectively. In group B, litters were joined two and two to pairs within experiments. In one litter of each pair (the reference litter), three animals were fed ad libitum. In the other litter (the linked litter), two (exp. 4) or three (exp. 5) animals were fed ad libitum. Restrictedly fed animals in a pair received 80% (exp. 4) or 74% (exp. 5) of the average intake of two randomly chosen ad libitum fed animals in the reference litter (the two reference animals) at the same average live weight. Group C consisted of animals from exp. 6, containing 33 litters, each with three barrows and three gilts. To about 48 kg live weight, animals in this group were fed ad libitum. Thereafter, two barrows and two gilts from each litter, randomly chosen, were fed restrictedly, one barrow and one gilt on 85% and one barrow and one gilt on 74% of the average ad libitum intake in experiments 1 to 5 at the same average live weight.

By this design, the variation in average daily food intake (FI) within, and the overlap between feeding levels was substantial (Kanis, 1988a). Therefore, animals fed a restricted diet were considered to belong to one feeding regimen, instead of different feeding levels. Thus, interactions with feeding regimen will be tested for two feeding regimens: ad libitum and restricted feeding. S*F interactions can only be studied in group C.

Animals were crossbreds (Dutch Yorkshire * Dutch Landrace), housed and fed individually. The food in exp. 1 to 4 contained 13.03 MJ digestible energy (DE) and 162 g crude protein (CP) per kg. In exp. 5 and 6, this was 13.41 MJ and 172 g for DE and CP, respectively. To correct for the small difference in energy content of the food between batches, food intake in batches 5 to 7 was multiplied by 1.029. Live weights of animals and food intake were recorded weekly. The growing period was from 27 to 107 kg live weight on average. At the end of the growing period, backfat thickness was measured ultrasonically and animals were slaughtered and dissected. The dissection method applied in group B was different from that in groups A and C. Background of the experimental designs, composition of the food mixture and dissection methods are given by Kanis (1988a and b).

Table 1. Experimental characteristics by group.

	Group		
	A	B	C
Experiments	1, 2 and 3	4 and 5	6
Sex (B=barrow, G=gilt)	B	B	B and G
No. of litters	70	56	33
Ad lib. fed animals per litter-sex combination	1	2 or 3	1
Restr. fed animals per litter-sex combination	2 or 3	2 or 3	2
Basis of restr. feeding[1]	1(r)	2(r) or 2(u)	scale

[1] For groups A and B, the number of ad libitum fed littermates (r) or unrelated animals (u) determining the food assigned to animals fed at a restricted level is given.

Correction for differences in degree of food restriction

FIC of littermates is positively correlated (Kanis, 1988b). Therefore, animals fed at a restricted feeding level in group A were, to some extent, fed according to FIC. In group B, only restrictedly fed animals in reference litters were fed according to FIC. Feeding of restricted animals in linked litters can be considered as scale feeding according to weight. Animals fed at a restricted level in group C were scale fed according to weight, starting at 48 kg live weight on average. The same scale was used for barrows and gilts.

For animals fed restrictedly, degree of food intake restriction (DFR) was calculated as $DFR = 1-(FI/FIC_1)$, where FIC_1 is the estimated food intake capacity, which is equal to the mean FI of ad libitum fed littermates of the same sex. In groups B and C, within feeding levels, the animals fed at a restricted level varied more in DFR relatively to FIC, than in group A. To study whether possible interactions between litter and feeding regimen could be caused by differences in DFR in groups B and C, production traits were corrected for these differences. Within experiment and sex, for each production trait the relative deviation (RD) compared with the average production of ad libitum fed littermates was calculated as:

$$RD_{ijk} = 1 - \frac{P_{ijk}}{AP_{ik}} \qquad (1)$$

where

RD_{ijk} = relative deviation for production trait i of restrictedly fed animal j in litter k,

P_{ijk} = actual value for production trait i of restrictedly fed animal j in litter k,

AP_{ik} = mean for production trait i of ad libitum fed animals in litter k.

Quadratic polynomial regression of RD on DFR, within experiment and sex, was used to adjust RD of animals fed at a restricted feeding level in groups B and C to the mean DFR for each experiment. From the adjusted RDs, adjusted production traits were calculated as:

$$TA_{ijk} = (1 - RDA_{ijk}) * AP_{ik} \qquad (2)$$

where

TA_{ijk} = production trait i of animal j in litter k, adjusted for differences in DFR,

RDA_{ijk} = RD_{ijk} from (1), adjusted for differences in DFR.

Statistical analysis

Significance of GEI was investigated for FI and for eight production traits defined by Kanis (1988a): average daily body-weight gain (DG), food conversion ratio (FCR), ultrasonically measured backfat thickness (BF), percentage lean parts (LP), percentage fatty parts (FP), lean tissue growth rate (LTGR), fatty tissue growth rate (FTGR) and lean tissue food conversion (LTFC). Analysis of variance was carried out with SAS GLM, type III (SAS Institute Inc., 1985).

For group A the model was:

$$y_{ijkl} = \mu + E_i + L_{j:i} + F_k + E{*}F_{ik} + L{*}F_{jk:i} + e_{ijkl} \qquad \text{(model 1)}$$

where

y_{ijkl} = trait of animal l on feeding regimen k in litter j in exp. i
μ = general mean
E_i = fixed effect of exp. i (i=1,3)
$L_{j:i}$ = random effect of litter j nested within exp. i
F_k = fixed effect of feeding regimen k (k=1,2)
$E{*}F_{ik}$ = fixed effect of interaction of exp. by feeding regimen
$L{*}F_{jk:i}$ = random effect of interaction of litter by feeding regimen within exp. i
e_{ijkl} = random error.

For group B:

$$y_{imjkl} = \mu + E_i + P_{m:i} + L_{j:im} + F_k + E{*}F_{ik} + P{*}F_{mk:i} + L{*}F_{jk:im} + e_{imjkl} \qquad \text{(model 2)}$$

where, in addition to model 1

$P_{m:i}$ = random effect of pair of litters m nested within exp. i (i=4,5)
$P{*}F_{mk:i}$ = random effect of interaction of pair by feeding regimen nested within exp. i.

For group C:

$$y_{njkl} = \mu + S_n + L_j + F_k + S{*}L_{nj} + S{*}F_{nk} + L{*}F_{jk} + e_{njkl} \qquad \text{(model 3)}$$

where, in addition to model 1

S_n = fixed effect of sex n (n=1,2)
$S{*}L_{nj}$ = random effect of interaction of sex by litter
$S{*}F_{nk}$ = fixed effect of interaction of sex by feeding regimen.

Significance of L*F, S*F and S*L interactions was tested against the error term. Significance of P*F interaction in model 2 was tested against the L*F interaction. Variance components were estimated for the random effects in models 1 to 3.

To quantify interactions, the ratio R was calculated as:

$$R = \sigma_I^2/\sigma_P^2$$

where

σ_I^2 = estimated variance component for a particular random interaction component

σ_P^2 = sum of estimated variance components for random effects.

Because $S*F_{nk}$ in model 3 was fixed, for this interaction only significance levels were calculated and no R values.

To investigate whether L*F interactions have effect on ranking of litters per feeding regimen, Spearman rank correlations were estimated between production traits of litters with ad libitum feeding and restricted feeding in each feeding level. Per group, average rank correlations, weighted for the number of litters in each feeding level, were calculated.

RESULTS

In Tables 2 and 3, the number of animals with complete records and the average production results are given by group, sex and feeding regimen, as well as the average feeding level as a proportion of ad libitum intake. Animals fed at a restricted feeding level in groups A and B received 76% of ad libitum on average. Food restriction in group C was less than in groups A and B because of ad libitum feeding in the first part of the growing period and the lower FIC of gilts. FI and DG in ad libitum fed animals were higher than found under practical conditions. The dissection method applied in group B was different from that in groups A and C, resulting in a higher lean parts percentage. Sex differences were as expected: barrows ate about 0.3 $kg.d^{-1}$ more food than gilts and had a higher FCR and more carcass fat when fed ad libitum. Under restricted feeding the sex difference was smaller for FI (because each sex was fed according to the same scale) and for most production traits.

Significance levels and R values of litter by feeding regimen (L*F), pair of litters by feeding regimen (P*F), sex by feeding regimen (S*F) and sex by litter (S*L) interactions in groups B and C are given in Table 4. In group A, all L*F interactions were non-significant with negative R values and are, therefore, not presented here. Significant L*F interactions and relatively

Table 2. Means ($\bar{x}$) and standard deviations (s) of food intake and production traits by feeding regimen in groups A and B.

	Group A				Group B			
	ad lib (n=68)		restr. (n=181)		ad lib (n=144)		restr. (n=135)	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Food intake (kg.d^{-1})	2.957	0.201	2.230	0.284	2.860	0.250	2.179	0.141
Feeding level[1)]	1.000	0.000	0.754	0.085	1.000	0.000	0.769	0.069
Daily gain (kg.d^{-1})	0.957	0.092	0.733	0.128	0.890	0.099	0.688	0.072
Food conversion ratio	3.103	0.232	3.075	0.262	3.228	0.234	3.189	0.260
Backfat thickness (mm)	19.30	2.84	16.03	2.80	16.25	3.15	14.09	2.78
Lean parts (%)	52.30	2.78	55.80	3.24	61.93	2.11	63.32	1.90
Fatty parts (%)	35.76	2.52	31.66	3.24	21.64	1.64	20.11	1.54
Lean tissue growth rate (kg.d^{-1})	0.378	0.043	0.312	0.051	0.432	0.044	0.343	0.037
Fatty tissue growth rate (kg.d^{-1})	0.316	0.041	0.210	0.046	0.180	0.028	0.126	0.018
Lean tissue food conversion	7.917	0.942	7.242	0.905	6.653	0.629	6.415	0.641

1) Proportion of ad libitum intake; for restrictedly fed animals calculated as actual average daily food intake, divided by average daily intake of ad libitum fed littermates.

Table 3. Means ($\bar{x}$) and standard deviations (s) of food intake and production traits by sex and feeding regimen in group C.

	Barrows				Gilts			
	ad lib (n=33)		restr. (n=61)		ad lib (n=32)		restr. (n=61)	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Food intake (kg.d^{-1})	2.931	0.212	2.454	0.141	2.617	0.220	2.392	0.138
Feeding level[1)]	1.000	0.000	0.844	0.079	1.000	0.000	0.922	0.083
Daily gain (kg.d^{-1})	0.939	0.076	0.784	0.073	0.875	0.093	0.787	0.071
Food conversion ratio	3.131	0.236	3.145	0.220	3.006	0.230	3.056	0.245
Backfat thickness (mm)	16.83	2.64	15.47	2.29	13.59	2.03	12.61	2.01
Lean parts (%)	55.21	3.11	57.14	2.47	58.68	2.21	59.91	2.44
Fatty parts (%)	34.06	3.01	31.82	2.44	30.51	2.27	29.09	2.31
Lean tissue growth rate (kg.d^{-1})	0.416	0.049	0.363	0.043	0.413	0.045	0.385	0.042
Fatty tissue growth rate (kg.d^{-1})	0.303	0.036	0.235	0.030	0.248	0.039	0.212	0.028
Lean tissue food conversion	7.131	0.892	6.845	0.756	6.395	0.687	6.280	0.712

1) Proportion of ad libitum intake; for restrictedly fed animals calculated as actual average daily food intake, divided by average daily intake of ad libitum fed littermates of the same sex.

high R values were found in group B for FI and growth rate traits (DG, LTGR and FTGR). In group C, the same traits showed significant S*F interactions, but L*F interactions were not significant in group C. Interactions of P*F in group B were significant for food conversion traits (FCR and LTFC). Interactions of S*L were never significant. For body composition traits (BF, LP and FP), no significant interactions were found, however, the R values of BF, LP and FP tended to positive values for S*L and P*F interactions.

Table 4. Significance levels (S)[1] of litter by feeding regimen (L*F), pair of litters by feeding regimen (P*F), sex by feeding regimen (S*F) and sex by litter (S*L) interactions, and their R values[2].

	Group B				Group C				
	L*F		P*F		L*F		S*F[3]	S*L	
	S	R	S	R	S	R	S	S	R
Food intake	***	0.343	NS	-0.132	NS	0.012	***	NS	-0.094
Daily gain	***	0.311	NS	-0.035	NS	-0.057	**	NS	-0.003
Food conv.	NS	0.005	*	0.182	NS	-0.032	NS	NS	0.001
Backfat th.	NS	-0.087	NS	0.039	NS	0.072	NS	NS	0.060
Lean parts	NS	-0.041	NS	0.028	NS	-0.112	NS	NS	0.007
Fatty parts	NS	-0.006	NS	0.032	NS	-0.097	NS	NS	0.039
LTGR	*	0.199	NS	0.067	NS	-0.018	*	NS	0.041
FTGR	*	0.169	NS	-0.025	NS	-0.157	***	NS	-0.037
LTFC	NS	-0.099	**	0.172	NS	-0.015	NS	NS	0.021

[1] NS = non-significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[2] R = ratio of variance components (see text).

[3] Fixed interaction effect, no R values.

Spearman rank correlations (weighted averages over feeding levels) between average ad libitum and restricted litter performances are in Table 5. In group A, Spearman rank correlations for growth rate and food intake traits were higher than in groups B and C, which was consistent with the significance of L*F interactions. The high rank correlation for FI in group A was expected because of the experimental design. For body composition traits, relatively high rank correlations were found, especially in group B. This confirms that L*F interaction was not important for body composition.

Table 5. Spearman rank correlations between performance of litters at ad libitum and restricted feeding (weighted averages per feeding level with n comparisons per group).

	Group		
	A (n=176)	B (n=56)	C (n=119)
Food intake	0.925	0.393	0.230
Daily gain	0.608	0.246	0.273
Food conversion ratio	0.275	0.285	0.202
Backfat thickness	0.302	0.586	0.312
Lean parts	0.512	0.707	0.476
Fatty parts	0.434	0.610	0.442
Lean tissue growth rate	0.402	0.103	0.315
Fatty tissue growth rate	0.682	0.362	0.385
Lean tissue food conversion	0.388	0.396	0.343

To investigate whether differences in DFR influenced interactions with feeding regimen as found in groups B and C, production traits of animals fed at a restricted feeding level were adjusted to the average restriction for each experiment, according to (1) and (2). Significance levels of interactions and R values in adjusted data are given in Table 6 and corresponding Spearman rank correlations in Table 7. In Table 6, no line for FI was entered because correction of FI for differences in DFR results in equal FIs for restrictedly fed littermates, and therefore in in-homogeneity of variances. As a control, correction for differences in DFR (over feeding levels, within experiments) was also carried out in group A, but that did not alter conclusions about interactions and rank correlations. Comparison of the results in Tables 6 and 7 with unadjusted results in Tables 4 and 5 shows that correction for differences in DFR completely removed the significance of L*F and S*F interactions. After correction, rank correlations were not much different between groups, except for body composition traits of which rank correlations were still somewhat higher in group B. This may be associated with the lower number of comparisons, or with the different dissection method as far as it concerns LP and FP.

Table 6. Significance levels (S)[1] of litter by feeding regimen (L*F), pair of litters by feeding regimen (P*F) and sex by feeding regimen (S*F) interactions, and their R values[2], after correction for degree of food intake restriction.

	Group B				Group C		
	L*F		P*F		L*F		S*F[3]
	S	R	S	R	S	R	S
Daily gain	NS	−0.049	NS	0.008	NS	0.004	NS
Food conv.	NS	0.026	+	0.107	NS	−0.047	NS
Backfat th.	NS	−0.081	NS	−0.000	+	0.097	NS
Lean parts	NS	−0.084	NS	−0.005	NS	−0.056	NS
Fatty parts	NS	−0.040	NS	−0.013	NS	−0.035	NS
LTGR	NS	−0.103	+	0.057	NS	−0.023	NS
FTGR	NS	−0.100	NS	0.002	NS	−0.040	NS
LTFC	NS	−0.095	*	0.101	NS	−0.022	NS

[1] NS = non-significant, + = $P < 0.1$, * = $P < 0.05$

[2] R = ratio of variance components (see text).

[3] Fixed interaction effect, no R values.

Table 7. Spearman rank correlations between performance of litters at ad libitum and restricted feeding, after correction for degree of food intake restriction (weighted averages per feeding level).

	Group		
	A	B	C
Food intake	1.000	1.000	1.000
Daily gain	0.618	0.665	0.607
Food conversion ratio	0.265	0.325	0.248
Backfat thickness	0.325	0.685	0.454
Lean parts	0.508	0.789	0.623
Fatty parts	0.447	0.737	0.563
Lean tissue growth rate	0.391	0.496	0.471
Fatty tissue growth rate	0.690	0.832	0.736
Lean tissue food conversion	0.400	0.458	0.400

DISCUSSION

Food intake

Results were in line with the literature, showing that genotype by feeding regimen interactions most frequently occur in traits concerning daily gain and food conversion. The present study indicates that FIC (or DFR) plays a role in these interactions. FIC of animals fed at restricted feeding levels was estimated as the average daily food intake of their ad libitum fed littermates. DFR relates actual restricted food intake to estimated FIC. The correlation of estimated FIC with true FIC is 0.3 to 0.4, depending on the number of animals per litter fed ad libitum (Kanis, 1988b). Despite this rather low accuracy, the effect of DFR on genotype by feeding regimen interactions was remarkable.

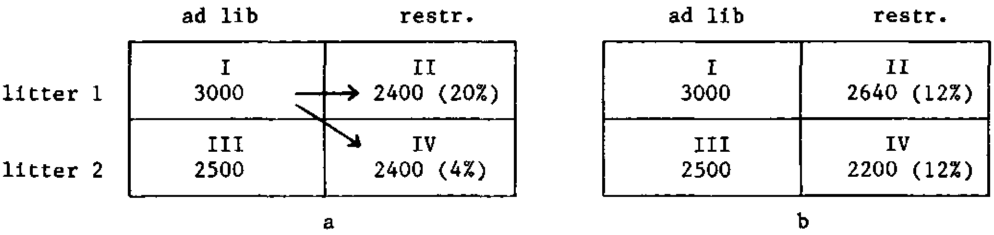
In group A, animals fed at a restricted level were fed according to FIC. Because food restriction was relative and not absolute, L*F interactions could be expected. However, for none of the traits those were significant. In group B, within a pair of litters, the restrictedly fed animals of each litter received food according to the ad libitum intake of one of the litters. Therefore, variation in restricted food intake between litters in a pair was less than variation in ad libitum food intake, causing the significant L*F interaction for FI. The P*F interaction for FI was not significant. Apparently, ad libitum fed animals in the linked litters did not influence the between-pair variance substantially. In group C, L*F interaction was expected because of the scale-type feeding of restrictedly fed animals. The R value of L*F interaction on FI was positive, but not significant, possibly due to the variation during ad libitum feeding in the first part of the growing period.

The S*F interaction on FI was highly significant because of the difference between gilts and barrows in ad libitum food intake, which could hardly be expressed during restricted feeding where each sex was fed according to the same scale. The results on S*F interaction were in line with results from Walstra et al. (1977) and from Campbell and King (1982).

Production traits

Interactions occurred most frequently in DG and its derived traits FCR, LTGR, FTGR and LTFC. In traits concerning body composition (BF, LP and FP) no interactions were found. The most logical explanation for this is the high correlation (about 0.8) between FI and DG (Kanis, 1988a). When interactions are found for FI, they can also be expected for associated traits. Correlations between FI and body composition traits were about 0.3, which seems too low for significant L*F interactions. The absence of significant interactions in group A, where littermates were fed on different feeding levels, but according to FIC, gave rise to the hypothesis that differences in DFR are a major source of genotype by feeding regimen interactions. The following explanation can be given.

It has been shown that FI and FIC are positively correlated with fatness of the carcass (Kanis, 1988b). Therefore, in the example given in Figure 1, which is illustrative for the experimental design in group B, animals in cell I (Figure 1a) have more fat than animals in cell III (difference in FI), and animals in II have more fat than animals in IV (difference in FIC). Apparently, this does not result in significant L*F interactions for body composition traits (Tables 4 and 5). For DG and its derived traits, the actual FI is predominant and a significant L*F interaction will be found. After correction of restrictedly fed pigs for differences in DFR, a situation similar to group A arises (Figure 1b). L*F interactions on FI and, therefore, on DG, LTGR and FTGR disappear because variation in DFR as source of interaction has been removed.



	ad lib	restr.
litter 1	I 3000	II 2400 (20%)
litter 2	III 2500	IV 2400 (4%)

a

	ad lib	restr.
litter 1	I 3000	II 2640 (12%)
litter 2	III 2500	IV 2200 (12%)

b

Figure 1. Example of food intake before (a) and after (b) correction for differences in degree of food intake restriction in two litters of one pair. Food intake in $kg.d^{-1}$, degree of restriction in parentheses. See text for explanation.

In fact the S*F interaction can be considered as an extreme illustration of what happens between animals or litters within sexes. Barrows have a higher FIC than gilts and are, therefore, more restricted when assigned to the same feeding regimen. Adjustment of FI to equal DFR, completely removes S*F interaction for production traits. This was also suggested by Donker et al. (1986). The same appears to hold for differences in DFR between litters. Correction of restricted food intake for these differences brings litters to the same DFR and, as a consequence, to a different FI within feeding regimens. As with L*F, also S*F interactions on production traits disappear after correction for differences in DFR.

Consequences for breeding

Genotype by feeding regimen interactions are likely to be an important part of the more general genotype by environment interactions (King, 1972). Existence of GEI makes pig-breeding programmes sub-optimal if GEI results in different rankings of genotypes in test environments compared with commercial environments (Brascamp et al., 1985). The present results showed that when litters are compared on ad libitum and on scale feeding, L*F and S*F interactions for traits such as daily gain and lean tissue growth rate can be expected. Probably these results can be extrapolated to breeding programmes where boars are selected in test-stations to produce progeny under practical conditions. Often in one or even in both environments, feeding is according to scale, not accounting for differences in FIC. In practice the easiest way to account for differences in FIC is to feed ad libitum in test-stations as well as under commercial conditions. Reports on poor genetic relationships between test-station results and on-farm or commercial data concern situations where one or both feeding regimens are not fully ad libitum (Standal, 1977; Ketelaars, 1979; Steane et al., 1984; Merks, 1988). It seems justifiable to conclude that differences in DFR are an important reason for the reported genotype by environment interactions.

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CHAPTER 4

THE COURSE OF DAILY GAIN, FOOD INTAKE AND FOOD EFFICIENCY IN PIGS DURING THE GROWING PERIOD

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Submitted for publication to Animal Production.
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ABSTRACT

The non-linear model y = a*exp(-b*W-c/W) was fitted to weekly calculated daily gain (DG), daily food intake (FI) and food efficiency (FE) of 653 barrows and gilts fed at ad libitum or restricted feeding levels during a growing period from 27 to 108 kg live weight. In this model, y is DG, FI or FE, W is live body weight and a, b and c are parameters. The model fitted well to the expected course of the traits, with an accuracy similar to that of quadratic polynomials. Parameters for one trait could simply be derived from the parameters for the other two traits. For each trait, four patterns were distinguished, depending on the signs of b and c. Curves with a maximum (b>0 and c>0), occurred most frequently. In cases of curves with a maximum, the model could be reparameterized to a model with parameters having a simple biological meaning.

Coefficients of determination in barrows averaged 0.29 for DG, 0.88 for FI and 0.45 for FE, whereas these values were somewhat lower in gilts. With ad libitum feeding, a DG curve with a maximum was fitted in 83% of the barrows and 61% of the gilts. The maximum DG was on average at live weights of 64 kg for barrows and 77 kg for gilts. A maximum in the FI curve was predicted in 60% of the barrows and 39% of the gilts. Curves for DG and FI in gilts were flatter than in barrows. FE curves, with ad libitum feeding, had a maximum in 59% of the barrows and 52% of the gilts. This predicted maximum FE was, on average, before the start of the growing period. Gilts had a higher FE than barrows from 35 kg body weight onwards, and the difference increased with increasing live weight. Differences in FE between ad libitum and restricted feeding were small, with a tendency for animals fed at a restricted feeding level to be more efficient at the end of the growing period.

Average FE curves and individual FI or DG curves were used for indirect prediction of individual DG or FI curves, respectively. The correlation between directly and indirectly predicted values of DG and FI at live weights of 30, 65 or 100 kg was about 0.7 in ad libitum fed barrows and gilts, and over 0.8 in pigs fed at a restricted level. This indicates that the model is suitable to predict and control the course of individual daily gain by influencing the course of food intake.

INTRODUCTION

Genetic variation in production traits of growing pigs not only exists for average levels, but also for changes of production traits during the growing period. Krieter (1986) showed that daily gain as function of live weight in Pietrain gilts, was less curved than in gilts of the German Landrace and the Belgian Landrace breeds, whereas the latter two breeds only differed in the level of daily gain. Vangen (1977) found a straighter curve for daily gain as a function of age in a line of Norwegian Landrace pigs selected for low daily gain and high backfat thickness compared with a line selected in the opposite directions and a control line. In an experiment with six lines of pigs, significant line effects on daily gain at all live weights from 30 to 95 kg were found. Contrasts in daily gain between lines depended on weight, indicating different growth patterns in the lines (Cöp and Buiting, 1977). In mice, it is possible to change the relative rate of growth to maturity, without changing mature weight (McCarthy and Bakker, 1979).

Concerning food intake, variation in level and course has been shown (Agricultural Research Council (ARC), 1981). Krieter (1986) found that differences in daily food intake between German Landrace and Pietrain were 8% at the beginning and increased to 19% at the end of the fattening period. For food conversion (food intake over body-weight gain), the relationship with live weight was linear in German Landrace and Belgian Landrace, whereas it was curvilinear (diminishing returns) in Pietrain. In mice, differences in curvature of daily gain, food intake and food efficiency (body-weight gain over food intake) were found between sexes and between lines selected for high postweaning gain, compared with unselected controls (Timon and Eisen, 1970).

Although variation between animals on a nucleus level is normally highly appreciated for breeding purposes, commercial farmers prefer uniform pigs. A pig producer, for instance, prefers equal daily gain for all pigs in a group in order to deliver them for slaughter at a similar weight at the same time. Therefore, it could be very useful to be able to control individual daily gain according to the mean level of the group or to the market requirements. With the development of automatic feeding gates, it will become possible to feed group-housed pigs individually.

In biological growth models, accurate functions to describe courses of production traits are needed (Moughan and Verstegen, 1987). These courses may also give additional tools for selection purposes (Parks, 1982; Krieter, 1986). Because of the strong relationships between daily gain, food intake and food efficiency, it may be possible to influence growth and food efficiency patterns by manipulating the food intake pattern, either by feeding management, or by selection. To do this, relationships between the courses of food efficiency, food intake and daily gain during the growing period must be known. The aim of this paper is to describe these courses and to discuss their relationships.

LITERATURE

In pigs, a growing period from 25 to 105 kg concerns only 25% of the possible weight gain, assuming a mature weight of about 320 kg (Walstra, 1980). Therefore, a useful model to describe courses of traits during the growing period requires knowledge of the concerning courses over longer ranges. Often information from other species can be used.

Growth curves and, to a lesser extent, food intake and food efficiency curves are often presented as a function of age because age can be recorded more easily and more precisely than weight. However, under normal circumstances, food intake and growth processes seem to be associated more functionally with body weight than with age (Timon and Eisen, 1970; Kielanowski, 1972; McCance and Widdowson, 1974; Wenk et al., 1980; Whittemore, 1983). Kanis (1983) found lower residual standard deviations for weekly ad libitum food intake in pigs as a function of weight, compared with the same function of age. Mostly, a significant curvilinearity is found in the relationship between weight and age in pigs during the growing period from 25 to 105 kg. However, the linear correlation between weight and age is very high (Cöp et al., 1970; Cöp, 1971; Flak et al., 1987). This means that patterns of most traits during the growing period are not much different when expressed as a function of weight compared with functions of age.

A quadratic polynomial can be used to describe daily gain (Krieter, 1986). However, such a parabola, although flexible, is symmetric around a vertical line through its maximum or minimum, and does, therefore, not give the best fit to data on gain per unit of time. This was shown by Taylor (1985) who found in genetic size scaling studies that growth as a function of degree of mature weight was skewed to the right. Moreover, with polynomials, extrapolation is not allowed and the parameters have no independent biological meaning if they are not orthogonalized.

Food intake per unit of time is often expected to increase after start of the growing period, following a diminishing-returns-type pattern for many species (Timon and Eisen, 1970; Neely et al., 1979; ARC, 1981; Krieter 1986), and reach an asymptote at or before mature weight (Parks, 1982). Tullis (1981) concluded that daily food intake increased linearly with live weight until about 85 kg and was constant at higher weights. Based on food-intake data in the growing period only, an acceptable asymptote often can not be estimated, and sometimes a maximum food intake seems to be followed by a decrease (Kanis, 1983). Taylor (1985) suggested that food intake of animals with a large appetite might decline after having reached a maximum. Fowler (1980) found that daily intake reached a peak at about 120 kg live weight and then declined slightly to very fluctuating values.

For food efficiency, Parks (1982) suggested a linear decrease with increasing live weight. Results of Taylor (1985) and Krieter (1986), however, indicate that the course of food efficiency is curvilinear. The results from Neely et al. (1979) were not consistent in showing a trend deviating from a linear decrease. In mice selected for high postweaning gain, Timon and Eisen (1970) found a maximum food efficiency shortly after weaning, followed by a decline.

From the literature it follows that, in pigs, daily food intake during the growing period has roughly the same pattern as daily gain in the first part of the growing period. The pattern of food efficiency looks similar to that of daily gain at the end of the growing period. Therefore, it would be possible to use the same model for each of the three traits. A suitable model should start from zero at very low body weights or ages (daily gain and food intake), reach a maximum (daily gain, possibly food intake) and decrease slowly to zero (daily gain, food efficiency), or show a diminishing-returns pattern (food intake) at higher live weights.

MATERIALS

Weekly live weight and food intake data were available from pigs, fattened in six experiments from 1976 to 1982 at the Agricultural University experimental station De Haar. Pigs were crossbreds between Dutch Yorkshire and Dutch Landrace, and were housed and fed individually with free access to water. Animals in experiments 1 to 5 were barrows, whereas those in experiment 6 were barrows and gilts from the same litters. Each experiment was considered as one batch, except experiment 6 where barrows and gilts were considered as two separate batches. The growing period was from 27 to 108 kg live weight, on average. In each of the seven batches, up to three animals per litter were fed ad libitum and two or three were fed restrictedly on different feeding levels. Number of litters per batch and assignment of animals to feeding levels are given by Kanis (1988). In batches 1, 2 and 3, animals fed at a restricted level received a fixed proportion (batches 1 and 2: 0.85, 0.74 or 0.65; batch 3: 0.85 or 0.74) of the food eaten by one, randomly chosen, ad libitum fed littermate at the same live weight. In batches 4 and 5, litters were paired at random. In each litter of a pair, animals fed at a restricted level received food according to the average ad libitum food intake of two randomly chosen reference animals in one litter of that pair. Restricted feeding levels were 0.80 (batch 4) and 0.74 (batch 5) of ad libitum. In batches 6 and 7, animals were fed ad libitum from 27 to 48 kg live weight. At this weight, in each batch two-thirds of the animals were switched to restricted feeding according to a fixed weight scale (0.85 or 0.74 of the average ad libitum intake in previous batches). These last animals were removed from the data because of the discontinuous food intake at 48 kg live weight and its possible impact on daily gain and food efficiency. The animals fed at a restricted feeding level in batches 1 to 5 were expected to have a normal food intake course.

The amount of food intended for each restrictedly fed animal was calculated on the basis of its own live-weight gain and the ad libitum food intake of its ad libitum fed reference animal(s) at similar weight(s). The food in batches 1 to 4 contained 13.03 MJ digestible energy (DE) and 162 g crude protein (CP) per kg. In batches 5 to 7, the food contained 13.41 MJ DE and 172 g CP per kg. To correct for the small difference in energy content of the food between batches, food intake in batches 5 to 7 was multiplied by 1.029.

The subset of 653 animals in 17 batch by feeding-level combinations was divided into three groups with similar treatments:

Group A: 249 barrows fed ad libitum in batches 1 to 6,
Group B: 33 gilts fed ad libitum in batch 7,
Group C: 371 barrows fed at restricted feeding levels in batches 1 to 5.

METHOD

The following non-linear model was chosen to fit to the data on daily gain (DG), daily food intake (FI) and food efficiency (FE) because of its simplicity and its attractive mathematical properties:

$$y_i = a * e^{-b*W_i - c/W_i} \qquad (1)$$

where

y_i = dependent variable (average daily gain, average daily food intake, or food efficiency) in week i,

W_i = live body weight in week i (average of weights at beginning and end of week i),

e = base of natural logarithm and

a, b and c are the parameters of the function.

Assuming $a>0$, and b and c non-zero, this function can show four basically different types of curves (see Figure 1):

type 1 ($b>0$ and $c>0$)

the function has a maximum of $y_{max} = a * e^{-2\sqrt{bc}}$ at $W_{max} = \sqrt{c/b}$, and is zero if $W \longrightarrow 0$ or if $W \longrightarrow \infty$,

type 2 ($b<0$ and $c<0$)

the function has a minimum of $y_{min} = a * e^{-2\sqrt{bc}}$ at $W_{min} = \sqrt{c/b}$, and is ∞ if $W \longrightarrow 0$ or if $W \longrightarrow \infty$,

type 3 ($b<0$ and $c>0$)

the function is zero if $W \longrightarrow 0$, or increases monotonically to ∞ if $W \longrightarrow \infty$,

type 4 ($b>0$ and $c<0$)

the function is ∞ if $W \longrightarrow 0$, or decreases monotonically to zero if $W \longrightarrow \infty$.

The mathematical interrelationships between the traits DG, FI and FE are easily covered by the model. Food efficiency for instance, can be fitted directly, but it can also be expressed indirectly into the parameters for DG and FI as:

$$FE = \frac{DG}{FI} = \frac{a_g}{a_f} * e^{-(b_g-b_f)W - (c_g-c_f)/W} \qquad (2)$$

where indices g and f refer to the parameters for daily gain and daily food intake. This is the same function as (1) and can also be fitted to food efficiency data directly. In a similar way, the parameters for each trait can be expressed in the parameters of the other two traits.

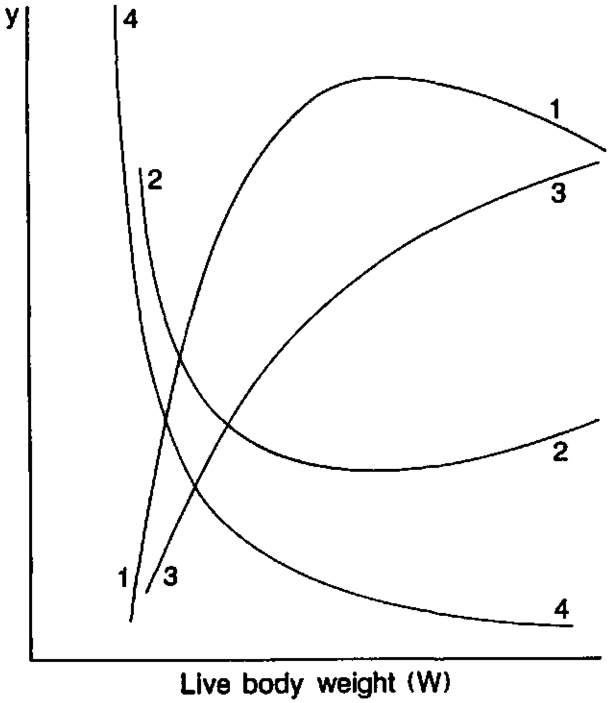

Figure 1. The four types of curves of the function $y = a*e^{-b*W-c/W}$ (see text for explanation of variables and parameters).

Model 1 was fitted to the data on DG, FI and FE according to a modified Gauss-Newton procedure with a BMD non-linear regression computer programme and the convergence criterion set to 0.00001 (Dixon, 1973). In some cases, 'atypical' types of curves showed up, due to one or two values with large deviations in combination with the relatively short growing period. For instance, at low body weights, DG and FI must be low and food efficiency should go to zero at live weights going to maturity. Therefore, to force possible atypical curves into a typical pattern, the parameter c was bounded to positive values for DG and FI, and the parameter b was bounded to positive values for FE. These bounds on the parameters resulted in type 1 and type 3 curves for DG and FI, and in type 1 and type 4 curves for FE.

To judge model 1, the results will be compared with a more familiar alternative, i.e. a quadratic polynomial (parabola):

$$y_i = b_1 + b_2 * W_i + b_3 * W_i^2 \qquad (3)$$

where y_i and W_i are the same as in (1), and b_1, b_2 and b_3 are parameters.

Goodness of fit was evaluated by means of residual standard deviations (RSD), coefficients of determinations (R^2) and Durbin Watson statistics (DBW), the latter giving an indication of first-order autocorrelation between residuals. DBW was calculated as:

$$DBW = \frac{\sum_{i=2}^{n} (e_i - e_{i-1})^2}{\sum_{i=1}^{n} e_i^2} \qquad (4)$$

where n is the number of data and e_i are the estimated residuals. If DBW>2, there is a tendency to a negative autocorrelation between the residuals, whereas if DBW<2, there is a tendency to a positive autocorrelation.

In contrast to polynomials, model 1 is non-linear and therefore the parameters of average curves for a group of animals are not the same as the averaged parameters of individual curves. To construct average curves, DG, FI and FE were predicted for each animal at every 5 kg from W=30 kg to W=100 kg on the basis of individual curves. Average group curves were fitted to the group means of these individual predicted values.

RESULTS AND DISCUSSION

Accuracy of the model

The data were based on weekly intervals which means that, for individual animals, particularly DG and FE, fluctuated highly between weeks. Nevertheless, all data on live weight and food intake were used as they were recorded, without any corrections or removal of outliers, and without any statistical weighing. One set of starting values for each trait was sufficient to allow the model converge in less than about 20 iterations, indicating that the model was very robust. Information about goodness of fit for model 1, without and with bounded parameters, and for the parabola is in Table 1. The distributions of the statistics in Table 1 were not significantly different from symmetric so that means can be used to judge the fit.

Table 1. Average residual standard deviations (RSD), coefficients of determination (R^2) and Durbin-Watson statistics (DBW) for model 1 with unbounded (1u) and bounded (1b) parameters, and for model 3, by trait and group. See text for models.

		Group[1)								
		A (n=249)			B (n=33)			C (n=371)		
Trait	Model	RSD	R^2	DBW	RSD	R^2	DBW	RSD	R^2	DBW
Daily gain ($kg.d^{-1}$)	1u	0.236	0.29	2.45	0.259	0.16	2.39	0.175	0.28	2.40
	1b	0.236	0.28	2.44	0.260	0.15	2.37	0.175	0.28	2.40
	3	0.234	0.29	2.46	0.258	0.17	2.40	0.174	0.29	2.41
Food intake ($kg.d^{-1}$)	1u	0.224	0.86	2.04	0.248	0.79	1.90	0.132	0.91	1.44
	1b	0.224	0.86	2.04	0.248	0.79	1.90	0.132	0.91	1.44
	3	0.222	0.86	2.06	0.251	0.78	1.91	0.129	0.91	1.47
Food efficiency	1u	0.075	0.47	2.52	0.091	0.36	2.50	0.074	0.42	2.46
	1b	0.075	0.46	2.51	0.092	0.35	2.49	0.074	0.42	2.46
	3	0.075	0.47	2.54	0.092	0.36	2.52	0.074	0.42	2.46

1) Group A: barrows fed ad libitum; Group B: gilts fed ad libitum; Group C: barrows fed at restricted feeding levels.

In general, model 1 (unbounded) and the quadratic polynomial did not differ in accuracy, although in the groups with the highest numbers of animals (groups A and C), there was a tendency for the polynomial to give a lower RSD and higher R^2. Relative to type 1 curves, a parabola tended to fit a higher maximum at a higher live weight than model 1. The effect of bounding the parameters and forcing the curves into a certain type was only noticeable in group B (the group with the highest frequency of atypical curves, as will be shown in Table 2). In general, those types of curves that were removed by bounding the parameters had higher RSD values, lower R^2 values and lower DBW values than the typical curves.

The Durbin Watson statistic (Table 1) indicated a tendency towards a positive autocorrelation for FI, but for DG and FE a more negative autocorrelation occurred. The strong indications for positive autocorrelation between the residuals for FI in group C can be due to too little flexibility of the model. However, RSD values in group C were low compared with groups A and B because feeding was at a restricted level and few food refusals occurred. Positive autocorrelation between residuals can be expected in particular with little weekly fluctuation. The relatively little fluctuation of FI in group C, within animals, between weeks, also caused a more consistent pattern for DG and FE, compared with groups A and B. This is reflected in the lower RSD values and higher R^2 values in group C. In ad libitum fed gilts (group B), the fits were less accurate than in ad libitum fed barrows (group A), also if in group A only the barrows from experiment 6 are considered. Gilts showed more fluctuation than barrows, particularly for daily gain. It is not clear whether this has a biological basis or is just due to chance because of the small number of gilts.

Table 2. Percentages of curve types, with unbounded (u) and bounded (b) parameters, by trait and group. See text and Figure 1 for curve types.

		Group 1)					
		A (n=249)		B (n=33)		C (n=371)	
Trait	Curve type	u	b	u	b	u	b
Daily gain	1	83.1	87.1	60.6	66.7	90.6	92.5
	2	8.0	-	24.2	-	4.9	-
	3	6.0	12.9	15.2	33.3	3.8	7.5
	4	2.8	-	-	-	0.8	-
Food intake	1	60.2	60.2	39.4	39.4	70.9	70.9
	2	2.4	-	9.1	-	-	-
	3	37.3	39.8	51.5	60.6	29.1	29.1
	4	-	-	-	-	-	-
Food efficiency	1	59.0	59.0	51.5	51.5	54.4	54.7
	2	13.3	-	27.3	-	12.1	-
	3	-	-	-	-	-	-
	4	27.7	41.0	21.2	48.5	33.4	45.3

1) Group A: barrows fed ad libitum; Group B: gilts fed ad libitum; Group C: barrows fed at restricted feeding levels.

Types of curves

Frequencies of the curve types, without and with bounds on parameters, are in Table 2. Type 1 growth (with a maximum) occurred most frequently. In the ad libitum fed gilts (group B), however, there was a tendency towards a flatter growth curve than in ad libitum fed barrows (group A), as illustrated by the higher frequency of type 2 and type 3 curves. For FI, type 1 and type 3 curves were predominant. In group A, 60% of the pigs had a food intake curve with a maximum, whereas this was only 40 % in group B. This indicates that gilts increased their food intake to a higher live weight than did barrows. For FE, type 1 curves were more frequent than type 4 curves. Putting bounds on the parameters forced all type 2 curves for FI, and almost all for FE, into type 3 curves. For DG, bounding gave more type 1 and more type 3 curves, resulting in a ratio of type 1 to type 3 curves of about 9:1 in groups A and C, and of about 2:1 in group B.

The percentages of the four major combinations of curve types for the three traits are in Table 3. The four combinations accounted for 80.9% of the pigs, with 36.8% having a type 1 curve for all three traits. The average frequency of each other combination was lower than 3.5%.

Table 3. Percentages of the major combinations of curve types by trait and group. See text and Figure 1 for types of curves.

	Traits[2]			Group[1]			
	DG	FI	FE	A (n=249)	B (n=33)	C (n=371)	Total (n=653)
Curve types	1	1	1	32.5	24.2	40.7	36.8
	1	1	4	18.1	6.1	22.4	19.9
	1	3	1	22.9	21.2	13.5	17.5
	1	3	4	5.2	3.0	8.1	6.7
	Total			78.7	54.5	84.6	80.9

[1] Group A: barrows fed ad libitum; Group B: gilts fed ad libitum; Group C: barrows fed at restricted feeding levels.

[2] DG: Daily gain; FI: Food intake; FE: Food efficiency.

In Table 4, means and standard deviations are given of individual predicted values at the start (W=30 kg), the middle (W=65 kg) and the end (W=100 kg) of the growing period for groups A and C, and for the ad libitum fed barrows and gilts in experiment 6. In general, the coefficients of variation were higher than 10%, especially at 30 and 100 kg live weight. Parameters of average curves for model 1 and coordinates of maximum values are in Table 5, the corresponding curves in Figure 2 and Figure 3. In groups A and C, average curves for all three traits were of type 1. The curves for DG in both groups showed the same pattern with a maximum gain at about 64 kg live weight. The level of group C was at about 80% of the level of group A. Average ad libitum food intake during the growing period showed a diminishing-returns type pattern. The maximum FI was predicted after the end of the growing period, on average. Pigs fed at a restricted feeding level received 78% of the ad libitum food intake, on average, but the relative difference between the food intake curves increased slightly with increasing live weights. Despite dif-

Table 4. Means of predicted values ($\bar{x}$) and standard deviations (s) at live weights of 30, 65 and 100 kg (y_{30}, y_{65} and y_{100}) by group and sex.

		Group 1)				Sex 2)			
		A		C		Barrows		Gilts	
		($\bar{x}$)	s	($\bar{x}$)	s	($\bar{x}$)	s	($\bar{x}$)	s
Daily gain	y_{30}	0.726	0.196	0.562	0.145	0.794	0.158	0.761	0.145
	y_{65}	1.005	0.121	0.794	0.122	1.016	0.110	0.913	0.112
	y_{100}	0.879	0.176	0.703	0.157	0.928	0.141	0.907	0.175
Food intake	y_{30}	1.711	0.270	1.361	0.210	1.707	0.262	1.708	0.237
	y_{65}	3.039	0.292	2.370	0.262	3.129	0.268	2.679	0.289
	y_{100}	3.468	0.384	2.636	0.337	3.453	0.323	3.165	0.362
Food efficiency	y_{30}	0.422	0.093	0.411	0.070	0.453	0.063	0.449	0.086
	y_{65}	0.330	0.029	0.333	0.027	0.327	0.031	0.339	0.033
	y_{100}	0.255	0.040	0.264	0.041	0.264	0.035	0.282	0.033

1) A: barrows fed ad libitum; C: barrows fed at restricted feeding levels.

2) Barrows and gilts from the same litters.

Table 5. Parameters of model 1 and coordinates of maxima for average curves[1] by group and sex.

Parameter		Group[2] A	Group[2] C	Sex[3] Barrows	Sex[3] Gilts
Daily gain	a (kg)	3.042	2.569	2.391	1.363
	b (kg^{-1})	8.651	9.233	6.765	2.572
	c (kg)	35.155	37.391	27.121	15.246
	DG_{max} ($kg.d^{-1}$)	1.004	0.793	1.015	0.917
	W_{max} (kg)	63.749	63.636	63.315	76.997
Food intake	a (kg)	5.833	4.815	7.285	3.486
	b (kg^{-1})	1.663	2.451	3.415	-1.295
	c (kg)	35.760	35.760	40.530	22.636
	FI_{max} ($kg.d^{-1}$)	3.591	2.664	3.462	n.d.
	W_{max} (kg)	145.888	120.794	108.938	n.d.
Food efficiency	a (kg)	0.547	0.538	0.393	0.387
	b (kg^{-1})	7.540	6.937	4.841	3.964
	c (kg)	1.093	1.901	-8.562	-7.881
	FE_{max} ($kg.d^{-1}$)	0.456	0.428	n.d.	n.d.
	W_{max} (kg)	12.040	16.554	n.d.	n.d.

[1] $b*10^3$; n.d. = not defined.

[2] A: barrows fed ad libitum; C: barrows fed at restricted feeding levels.

[3] Barrows and gilts from the same litters.

ferences in DG and FI between groups A and B, the curves for FE were similar. There was, however, a tendency for ad libitum fed pigs (group A) to be more efficient in the beginning of the growing period and for restrictedly fed pigs (group C) to be more efficient at the end. In each group a maximum FE was predicted before the start of the growing period.

Barrows had a higher maximum DG than gilts, and this maximum was reached at a lower live weight than in gilts (Table 5 and Figure 3). Beyond the maximum, barrows showed a larger decline in weight gain than the gilts. This was also confirmed by the fact that 60% of the ad libitum fed gilts had a DG curve of

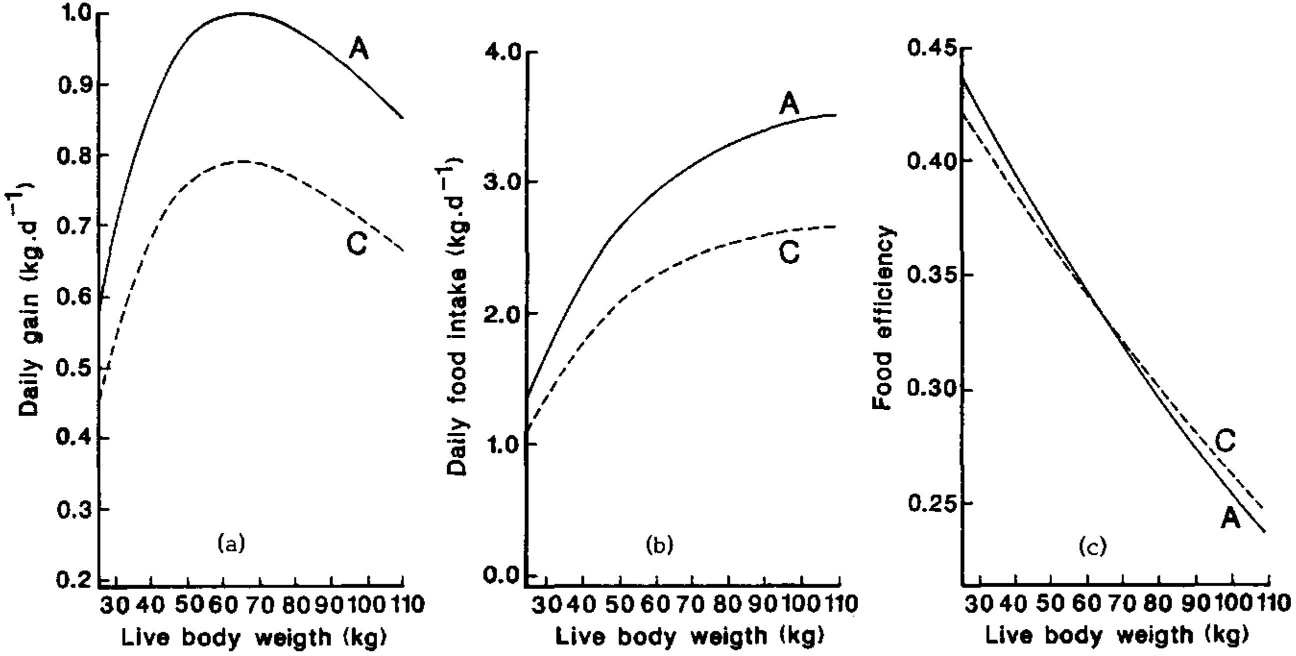

Figure 2. Average courses of daily gain (a), food intake (b) and food efficiency (c) during the growing period for barrows fed at ad libitum (group A) and restricted feeding levels (group C).

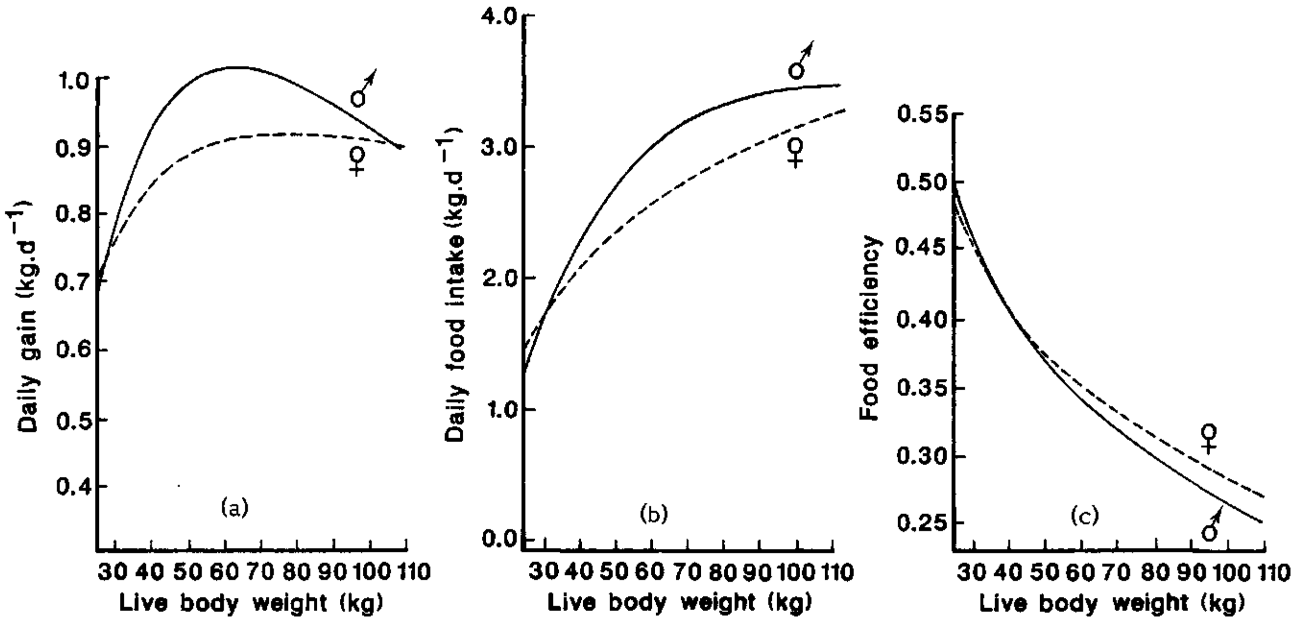

Figure 3. Average courses of daily gain (a), food intake (b) and food efficiency (c) during the growing period for barrows (♂) and gilts (♀) fed ad libitum.

type 1, whereas 83% of the ad libitum fed barrows had a type 1 curve (Table 2). The increase in FI in the first half of the growing period was higher for barrows than for gilts. In barrows, however, the FI curve showed a plateau in the second half, with a maximum at 109 kg live weight (Table 5), whereas the gilts continued to increase their FI. From about 35 kg on, the FE in gilts was higher than in barrows, and this difference increased with increasing live weight (Figure 3).

Relationships between traits

If the curve for FE would be known, the curve for DG could be indirectly predicted according to (2) from the curve of FI and vice versa. This is important for the appraisal of feeding strategies of groups of pigs and even of individual pigs in a group, if individual feeding can be applied. However, individual FE curves are not known beforehand and therefore suitable standard FE curves must be used.

In this study the mean FE curve of a batch by feeding-level combination was used as a standard curve for each pig belonging to that combination. Average directly and indirectly predicted values at 30, 65 and 100 kg live weight were compared in each group. Differences between group means of directly and indirectly predicted values for DG and FI appeared to be non-systematic, and were always lower than 2%. In Table 6, the within group correlations are given between directly and indirectly predicted values (indicated by subscripts 'dir' and 'indir'). If FE is taken as a constant, then DG_{indir} is equal to that constant multiplied by FI_{dir}. The correlation between DG_{dir} and DG_{indir} is then equal to the correlation between DG_{dir} and FI_{dir}. The same holds for the correlation between FI_{dir} and FI_{indir}. Therefore, correlations between DG_{dir} and FI_{dir} are also in Table 6. In group B, these were indeed equal to the correlation between directly and indirectly predicted DG and FI because group B consisted of only one batch by feeding-level combination.

Correlations between directly and indirectly predicted values were quite high in each group, ranging from about 0.60 to 0.85, with a mean of 0.73. These correlations were about the same magnitude as the correlation between average DG and average FI.

The results indicate that it is not only possible to predict average DG or average FI from average FE, but that there are also good possibilities to predict the courses of DG or FI during the growing period, from an appropriate but fixed course of FE and a known food intake scheme or a desired pattern of daily gain.

Table 6. Correlations between directly and indirectly predicted traits at 30, 65 and 100 kg live weight (y_{30}, y_{65} and y_{100}) by group.

Traits 2)		Group 1) A	B	C
DG_{dir}, DG_{indir}	y_{30}	0.77	0.65	0.88
	y_{65}	0.75	0.69	0.89
	y_{100}	0.74	0.82	0.79
FI_{dir}, FI_{indir}	y_{30}	0.64	0.65	0.82
	y_{65}	0.74	0.69	0.86
	y_{100}	0.73	0.82	0.75
DG_{dir}, FI_{dir}	y_{30}	0.59	0.65	0.83
	y_{65}	0.72	0.69	0.88
	y_{100}	0.73	0.82	0.78

1) Group A: barrows fed ad libitum; Group B: gilts fed ad libitum; Group C: barrows fed at restricted feeding levels.

2) DG: Daily gain; FI: Food intake.

GENERAL DISCUSSION

Polynomials have been used extensively to describe DG, FI and FE in pigs during a normal growing period (see for instance Krieter, 1986). However, the present function (1) has more attractive mathematical properties and it probably fits the expected biological changes in the traits better over a longer period. If body weight is close to zero, the function value is zero and it can increase very slowly at low body weights, which is expected for DG and FI (types 1 and 3 curves). After a weight range with increasing responses, the function reaches an inflexion point followed by a diminishing response to increasing live weight. This part is quite suitable for fitting DG and FI, but not for fitting FE. The function may then reach a maximum (DG) or a plateau (FI). After a maximum the function values may decrease slowly (DG) or faster (FE), going to zero as body weight increases. This last part is the only imperfection of the model, because DG and FE are expected to be zero at the (finite) mature weight. However, this does not influence the present conclusions, because mature weight is much higher than slaughter weight.

The frequency of atypical curves may be considered as quite high, especially in ad libitum fed animals. This is not a shortcoming of the model, but rather because data were used as measured, including outliers. In addition, there is a higher risk of type 2 curves when there is no clear curved trend as was the case with some gilts. It should also be noted that animals in group C were fed restrictedly according to ad libitum food intake of one or two animals in the same batch. This, in addition to the low amount of refused food, caused some smoothing of the FI curves in group C. Therefore, the types of curves found in group C can be considered as good indicators of the types of curves for ad libitum feeding.

In cases of type 1 curves (by far the most frequently occurring type for each of the three traits, except FI for group B), the model can be reparameterized to parameters with a clear biological meaning as:

$$y_i = y_{max} * e^{-(W_i - W_{max})^2/(d * W_i)}$$

where y_{max} and W_{max} are direct estimates of the coordinates of the maximum, and d (equal to 1/b in function (1)) is associated with the peakedness of the curve (larger d, less peaked). Moreover, the fact that the ratio of two functions (1) results in the same function (2) makes the model attractive for describing the combination of DG, FI and FE.

In general, the shape of the curves for DG, FI and FE as presented in Figures 2 and 3, agreed with the literature if compared at the same weight range. The maximum DG and FI in the gilts were somewhat higher than found by Krieter (1986), based on quadratic and cubic polynomials. This could be due to the relatively small number of gilts in the present study. The curvilinear relationship of FE with live weight corresponds well to the linear relationship for food conversion ratio found by Krieter (1986). ARC (1981) evaluated food intake results from different experiments and concluded that the functions: digestible energy (DE in $MJ.d^{-1}$) = $3.00*W^{0.63}$ and DE = 55(1-exp(-0.0204*W)) described food intake well. Each function is of the diminishing-returns type, with the latter having an asymptote at 55 ($MJ.d^{-1}$). Predicted FI at W=100 kg is about 4.2 $kg.d^{-1}$ for the former and 3.7 $kg.d^{-1}$ for the latter function.

This is higher than in the present experiment, probably because in few of the experiments evaluated by ARC (1981) pigs were taken to weights greater than 90 kg.

The effect of sex on the FI curve was also found by Kanis (1983) in the same material, but with different models. Probably the effect of sex on the curves for DG and FE is associated with the effect of sex on the curve for FI. It is well known that gilts are leaner than barrows. This may be related to the shape of their FI curve, which is flatter, on average, with less curvature and no maximum.

Results indicate that it is possible to indirectly predict the course of DG from alternative feeding regimens on the basis of parameters for a standard FE curve. This makes the model, in principle, suitable for use in optimizing feeding strategies and management programmes.

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CHAPTER 5

OPTIMIZATION OF SELECTION FOR FOOD INTAKE CAPACITY IN PIGS

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To be submitted for publication in Animal Production.
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ABSTRACT

Optimal selection directions for average ad libitum food intake capacity (FIC) in growing pigs were derived by means of a biological growth model based on the linear/plateau relationship between protein deposition and food intake. Input variables for the model were: minimum fat to protein deposition ratio (R), maximum protein deposition rate (Pd_{max}) and food intake (FI). Output variables were production traits and production costs.

Economic values were estimated for breeding goal traits R, Pd_{max} and FIC, at three alternative levels of FIC. If FIC was too low to realize Pd_{max}, the economic value of FIC was about 100 Dfl. per $kg.d^{-1}$ and optimal selection emphasis should be mainly on FIC, resulting in a rapid increase of daily weight gain (DG). If FIC was higher than necessary to realize Pd_{max}, the economic value of FIC was about -40 Dfl. per $kg.d^{-1}$, and short-term selection resulted in increase of carcass leanness but decrease of FIC and DG. If FIC was just sufficient to realize Pd_{max}, the lowest production costs occurred, and selection should be for R and Pd_{max}. In this third alternative, the gain in FIC should follow the gain in R and Pd_{max} in an optimal way and selection should best be carried out with a desired gains index, which resulted in improvement of DG and carcass leanness. It was shown that, in cases where FIC was higher than necessary to realize Pd_{max}, selection with a desired gains index should be preferred because this was more profitable in the long term. From the model calculations, it followed that future profit from selection of growing pigs for production traits is likely to decline because of the necessity to increase FIC.

In the second part of this study, the relationship between the shape of the food intake curve and production traits was investigated. After correction for variation in average daily FI, more curvature of the food intake curve appeared to be associated with a lower DG and a higher food conversion ratio. A high food intake at the end of the growing period (with the same FI) was favourable for DG and for carcass leanness.

To achieve optimal results in pig meat production, accurate tuning of selection procedures and feeding regimens on the biological possibilities of the pig will be necessary. More knowledge is required concerning the genetic background of protein deposition.

INTRODUCTION

Index selection for production traits in pig breeding programmes may result in a decrease in food intake capacity (Smith and Fowler, 1978; Mitchell et al., 1982; Ellis et al., 1983; Hong, 1985; Brandt et al., 1985; Webb and Curran, 1986). This is probably caused by the relatively high economic value for carcass leanness and for food conversion compared with that for daily gain. Future improvement in overall economic value from reduction in fatness and in voluntary food intake is expected to be limited. In the long term, improvement should come from increase in the rate of lean tissue deposition, which must be accompanied by an increase in appetite (Fowler, 1986; Webb, 1986). Therefore, there is general agreement that food intake capacity (FIC) must not decrease further in order not to limit genetic response for lean tissue growth rate.

How to select for FIC in combination with production traits is unclear. With selection under ad libitum feeding, the chance of a decrease in FIC may be higher than with restricted feeding (Fowler et al., 1976; McPhee et al., 1979). However, FIC can only be measured directly with ad libitum feeding. Kalm and Krieter (1985) and Krieter (1986) discussed four genetic ways to avoid a further decline of food intake capacity:

1. Restricted selection index with response for daily food intake restricted to zero change.
2. Higher economic weight on daily gain.
3. Selection for lean tissue growth rate.
4. Different weights on food intake in different parts of the growing period (higher at the beginning, lower at the end).

Krieter (1986) stated that at present the simplest way to counterbalance reduction in food intake is to put more emphasis on growth rate. According to Brandt (1987), direct use of food intake in a selection index is not possible because there is no economic weight available for this trait. Therefore, the best way at present should be to use a selection index that does not change food intake. The expected genetic progress would be reduced by only 0 to 11.8%, depending on breed and type of index (Brandt, 1987). However, the expected progress in meat percentage was much reduced, whereas the expected progress in daily gain was drastically increased. In The Netherlands, the trait 'ad libitum food intake' is incorporated into the breeding goal of the pig herdbooks, as well as into the selection index. (Knap et al., 1985). The economic weight for food intake is relatively small and negative, but the response from selection is expected to be positive.

Food intake during the growing period is rather variable between animals, especially with respect to reaching a maximum or a plateau at higher weights (Kanis and Koops, 1988). It is not known what the most desirable form is of the food intake curve, with respect to production traits. Selection for voluntary food intake, directly or indirectly, may have an influence on the form of the food intake curve and therefore on production traits.

Recently, biological growth models with mainly nutritional objectives have been developed for pigs (Whittemore, 1983; Moughan and Smith, 1984; Black et al., 1986). However, Moughan and Verstegen (1987) mentioned additional objectives for growth models: 'to aid calculation of the relative economic values of unit improvement in genetic selection traits' and 'to provide information on the physiological consequences of genetic improvement and to afford analysis of the effects on animal performance from genetic improvement of basic physiological traits'.

The first aim of this paper is to estimate economic values of FIC (defined as average daily ad libitum food intake) by means of a biological growth model and to present a method to optimize selection for FIC. The second aim is to give more insight into the relationship of different forms of food intake curves with production traits.

MODEL CALCULATIONS

Description of the growth model

Metabolizable food energy was assumed to be partitioned between energy for maintenance, protein deposition and fat deposition. Maintenance requirement per day (E_m) was expressed as a function of body protein mass (Pt in kg) according to Whittemore (1983):

$$E_m \text{ (MJ ME.d}^{-1}) = 1.85 * Pt^{0.78} \qquad (1)$$

Average maintenance requirement during the growing period is:

$$\bar{E}_m = \int_{t_0}^{t_1} 1.85 * Pt^{0.78}\, dt/(t_1-t_0)$$

where t_0 and t_1 are first and last day of the growing period, respectively.

Protein deposition with ad libitum feeding is fairly constant during large parts of the growing period (Cöp, 1974; Tullis, 1981; Moughan and Verstegen, 1987). Assuming that protein gain is constant during the entire growing period from 25 to 105 kg, average daily maintenance requirement during the growing period can be expressed in terms of Pt_0 and Pt_1 analogous to Foster et al. (1983) as:

$$\bar{E}_m = \int_{Pt_0}^{Pt_1} 1.85 * Pt^{0.78}\, dPt/(Pt_1-Pt_0)$$

$$= (1.85/1.78) * (Pt_1^{1.78} - Pt_0^{1.78})/(Pt_1-Pt_0) \qquad (2)$$

where Pt_0 and Pt_1 are protein mass at first and last day of the growing period, respectively.

It was assumed that protein and fat deposition depend only on energy intake. The supply of amino acids, minerals, vitamins etc. is assumed to be always sufficient. The linear/plateau form was adopted for the relationship between daily protein deposition and energy intake (Whittemore and Fawcett, 1976; Whittemore, 1983; Campbell et al., 1985b). If the composition of the food is fixed, Pd is related to daily food intake (FI) as presented in Figure 1. For energy requirement of protein and fat deposition, efficiencies given by Moughan and Smith (1984) and Metz et al. (1986) were used. It was assumed that protein and fat contain 23.8 and 39.6 $MJ.kg^{-1}$, respectively, and are deposited with efficiencies of 0.45 (k_p) and 0.75 (k_f). This means that for protein and fat deposition, 53 MJ metabolizable energy per kg is needed (b_f= b_p= 53 MJ ME per kg). It was assumed in the model that protein deposition (Pd in $g.d^{-1}$) is always accompanied by deposition of a certain amount of fat (Ld in $g.d^{-1}$). The minimum ratio of fat to protein deposition is R. In Figure 1, the minimum FI to realize the maximum Pd (Pd_{max}) is FI_o, and FI with Pd=0 is M. If FI is between FI_o and M (indicated as $FI<FI_o$), then the amount of fat deposited will be R*Pd, and the regression of Pd on FI ($tg\alpha$) is:

$$tg\alpha = EDF/(b_p + R*b_f) \qquad (3)$$

where EDF is energy density of food (metabolizable energy). For EDF, 12894 kJ ME per kg food was taken (Kanis, 1988a). With b_f= b_p= 53, $tg\alpha = 243.28/(1+R)$. If FI is higher than necessary to realize Pd_{max} ($FI>FI_o$), then the amount of fat deposited is greater than R*Pd. Average values vary between 0.6 and 1.2 for R, and between 100 and 160 $g.d^{-1}$ for Pd_{max} (Whittemore, 1983).

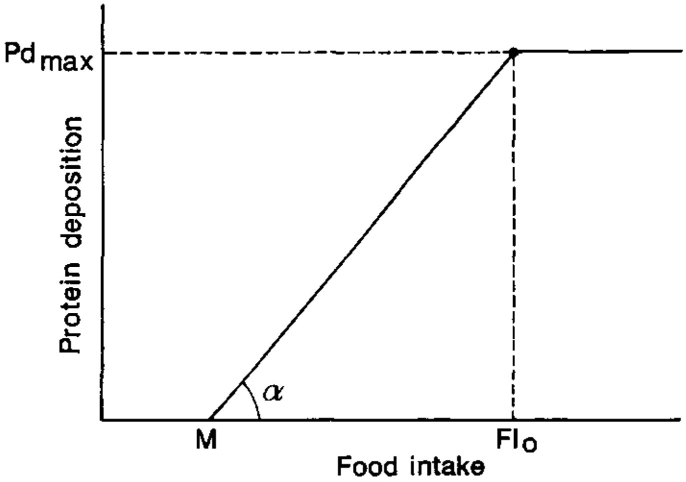


Figure 1. The linear/plateau relationship between protein deposition and food intake. M is food intake with zero protein deposition and FI_0 is minimum food intake to realize maximum protein deposition (Pd_{max}).

The following constants were adopted for the relation with body-weight gain and body composition:

- Empty body weight (EBW) = 0.95 * live body weight (LBW) (according to Whittemore (1983), 5% gut fill was assumed).
- Lean body mass (LBM) = EBW - total fat mass = 4.35 * Pt (Metz et al., 1986)
- Carcass weight = 0.77*LBW (dressing % = 77; Walstra, 1980).
- Lean weight in the carcass = 0.58 * LBM (Whittemore, 1983).
- Fat mass at beginning of growing period = 0.15 * EBW (Whittemore, 1983).

The following production costs (in Dutch guilders (Dfl.) under Dutch circumstances) were assumed (De Vries, 1987):

- Fixed costs per pig: 155.00.
- Variable costs (excluding food): 0.40 per pig per day.
- Food costs: 0.53 per kg of food.

For lean meat percentage in the carcass, each percent deviation from 52% was assumed to give differential income (positive or negative) of Dfl. 0.04 per kg carcass weight (De Vries, 1987). Total corrected production costs per pig were calculated by subtracting this differential income from the total production costs.

Calculation procedures

For specified combinations of R, Pd_{max} and FI, the maximum possible protein mass at the end of the fattening period is calculated first. This maximum Pt depends only on R and occurs if FI is less than or equal to the amount necessary to realize Pd_{max}. Substitution of maximum Pt into (2), gives maximum average daily maintenance requirement. If energy intake for production is not sufficient to realize Pd_{max}, Pd and Ld are calculated as:

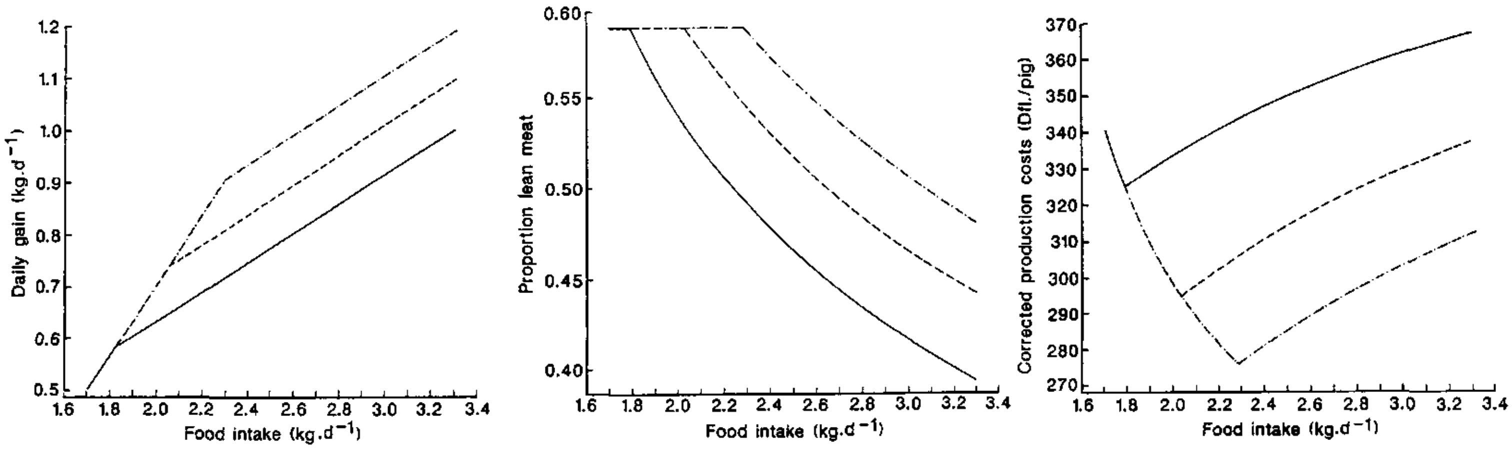
$$Pd = E_{prod}/(b_p+R*b_f) \qquad (4)$$

$$\text{and } Ld = R*Pd \qquad (5)$$

where $E_{prod} = EDF*FI-\bar{E}_m$. If energy intake is sufficient to realize Pd_{max}, then fat deposition and maintenance requirement are calculated iteratively by stepwise increasing Ld and, consequently, decreasing Pt_1 and $\bar{E}_m$ until total energy intake meets energy requirement. Finally, performance traits and production costs are calculated.

Results

The effects of FI on average daily gain (DG), proportion lean meat (LP) and total corrected production costs per pig (CPC) are presented in Figure 2 for R=1 and Pd_{max} is 100, 130 or 160 $g.d^{-1}$. The break-points in the curves coincide with FI_o, which corresponds to the FI with the lowest calculated food conversion ratio (FCR), lowest lean tissue food conversion (LTFC) and lowest CPC. From FI_o onwards, an increasing FI is associated with a decreasing LP. The effect of a higher Pd_{max} is that FI_o occurs at a higher FI and is accompanied with lower costs. The effect of one unit increase of FI on CPC with fixed R and Pd_{max} (economic value) can be derived from Figure 2c. The economic value of FI (with ad libitum feeding FIC) depends on the location of the break-point in the Pd curve. If $FIC<FI_o$, then the economic value is positive; it is negative if $FIC>FI_o$. If $FIC<FI_o$, then an increase of average FIC of 0.1 $kg.d^{-1}$ reduces CPC by about 10 Dfl. (at R=1 and FIC=2), which corresponds to an economic value for FIC of 100 Dfl. per $kg.d^{-1}$. This value is higher at low levels of R and FIC, and does not depend on Pd_{max}. If $FIC>FI_o$, the economic value of FIC is about -40 Dfl. per $kg.d^{-1}$ (with Pd_{max}=130 and FIC=2.3). This value does not depend on R, and becomes less negative at higher levels of FIC and more negative at higher values of Pd_{max}.



(a) (b) (c)

Figure 2. Effects of food intake on average daily gain (a), proportion lean meat (b) and total corrected production costs (c), for three levels of maximum protein deposition (Pd_{max}), with minimum fat/protein deposition ratio (R) equal to 1.0.

——— : Pd_{max}=100 g.d^{-1}, -------- : Pd_{max}=130 g.d^{-1}, -.-.-.-. : Pd_{max}=160 g.d^{-1}.

The effect of Pd_{max} on CPC, with different FICs is in Figure 3 (R=1). If $FIC<FI_0$ (e.g. FIC=1.7 $kg.d^{-1}$ and $Pd_{max}>90$ $g.d^{-1}$), then the economic value of Pd_{max} is zero because Pd_{max} has no effect on Pd with low FI. If $FIC>FI_0$, the economic value of Pd_{max} depends on the level of Pd_{max} and the level of FIC (higher at lower levels). A value of 1 Dfl. per $g.d^{-1}$ appears to be reasonable for the economic value of Pd_{max} (with Pd_{max}=130 and FIC=2.3).

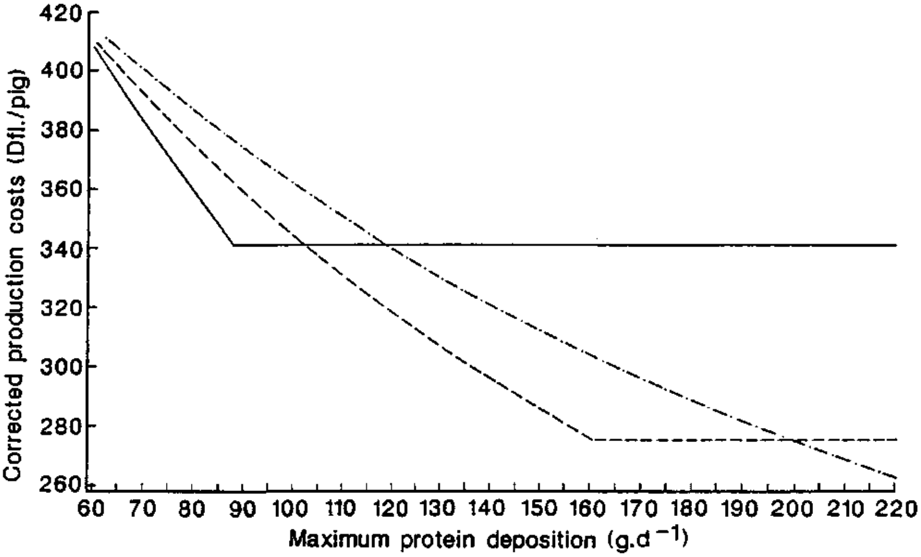


Figure 3. Effect of maximum protein deposition on corrected production costs for three levels of food intake capacity (FIC) and minimum fat/protein deposition ratio equal to 1.0. ———— : FIC=1.70 $kg.d^{-1}$, -------- : FIC=2.30 $kg.d^{-1}$, -·-·-·-· : FIC=3.00 $kg.d^{-1}$.

The effect of R on CPC is in Figure 4 (for Pd_{max}=130, FIC=1.8; Pd_{max}=130, FIC=2.6 and Pd_{max}=160, FIC=2.6). R has effect on Pd if $FIC<FI_0$ (see Figure 1), so that the economic value of R is non-zero if $FIC<FI_0$ (e.g. FIC=1.80 $kg.d^{-1}$ and Pd_{max}=130 $g.d^{-1}$). If $FIC>FI_0$ (e.g. FIC=2.60 $kg.d^{-1}$ and Pd_{max}=160 $g.d^{-1}$) and R<1.5, then the economic value of R is zero because R has no effect on Pd. With increasing R, FI_0 also increases so that FIC may become less then FI_0, which results in a non-zero economic value for R. At R=1, Pd_{max}=130 and FIC=1.8, the economic value of R is about -70 Dfl. per unit, which becomes more negative at lower values of R.

The economic values above hold (given the assumptions in the model) for ad libitum feeding (FI=FIC) under commercial conditions. If FIC>FI_0, then restricted feeding can be economically attractive. Assuming that the (restricted) feeding level is always kept at the optimum (FI=FI_0), economic values for Pd_{max} and R can be derived for restricted feeding. An increase of Pd_{max} from 130 to 131 $g.d^{-1}$, with R=1, decreases minimum production costs from about 294.50 to about 293.70 Dfl., which corresponds to an economic value of 0.80 Dfl. per $g.d^{-1}$. This is lower than with ad libitum feeding for FI<FI_0 because FI should increase with increasing Pd_{max} and fixed R. Similarly, the economic value of R, with Pd_{max}=130, is about -23 Dfl. per unit. This is less negative than with ad libitum feeding for FIC<FI_0 because Pd does not increase with increasing R and daily gain decreases due to the lower FI. With restricted feeding, the economic value of FIC is zero if FIC>FI_0.

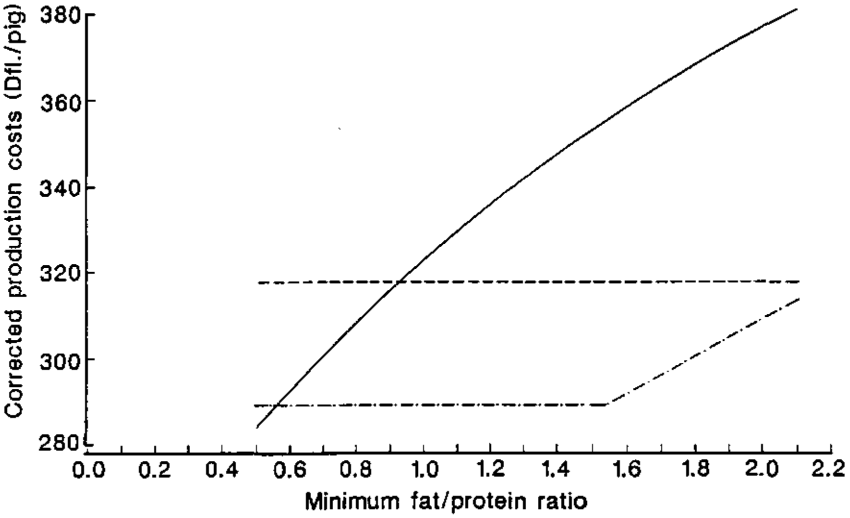


Figure 4. Effect of minimum fat/protein deposition ratio on corrected production costs for three combinations of maximum protein deposition (Pd_{max}) and food intake capacity (FIC).

———— : Pd_{max}=130 $g.d^{-1}$, FIC=1.80 $kg.d^{-1}$.

-------- : Pd_{max}=130 $g.d^{-1}$, FIC=2.60 $kg.d^{-1}$.

-·-·-·-· : Pd_{max}=160 $g.d^{-1}$, FIC=2.60 $kg.d^{-1}$.

SELECTION INDEX

Traits and parameters

To demonstrate selection for FIC in combination with production traits, a selection index was developed. In harmony with the biological model, R, Pd_{max} and FIC were chosen as the genetically determined traits to select for. A testing system with ad libitum feeding was assumed, with two littermates of which one is slaughtered at the end of the test to supply additional information on LP. The selection index included DG, FIC and ultrasonically measured backfat thickness (BF) for each full sib, and LP for the slaughtered animal.

Although it can well be defended on theoretical grounds that genetic parameters are different for populations with $FIC<FI_0$, $FIC=FI_0$ or $FIC>FI_0$, only one set of phenotypic and genetic parameters was used. Parameters for ad libitum feeding from the literature will mostly concern situations with $FIC>FI_0$, whereas parameters for restricted feeding will more often cover $FIC<FI_0$. Therefore, for index traits the parameters used are mainly rounded averages from literature sources with ad libitum and restricted feeding (Blum, 1983; Sönnichsen, 1983; Hong, 1985; Knap et al., 1985; Krieter, 1986; Johansson et al., 1987). Genetic correlations (r_g) are taken equal to phenotypic correlations (r_p) for all traits, which seems to be an acceptable simplification, at least for the index traits. The complete parameter set used in this model study is in Table 1.

For R and Pd_{max}, no direct information about parameters is available, so indirect information was used. For restricted feeding, Cöp (1974) gave a heritability (h^2) of 0.18 for Pd in pigs, whereas More O'Ferral et al. (1968, cited by Cöp, 1974) found in mice $h^2=0.09$. Cöp concluded that perspectives for selection for protein deposition are not very good. Recent estimates for h^2 of lean tissue growth rate (LTGR) are generally higher than 0.2: Blum (1983) found 0.21, Krieter (1986) 0.45 and Johansson et al. (1987) on average about 0.35. However, LTGR and Pd are not equal because the trait LTGR mostly contains some growth of fat and bone, which probably have a higher h^2 than protein deposition (Sönnichsen, 1983; Krieter, 1986). Moreover, only 55% of protein is deposited in carcass muscles (Just and Pedersen, 1976). In the present study, $h^2=0.2$ was assumed for both protein deposition traits R and Pd_{max}.

It was suggested by Whittemore (1983), and confirmed by Campbell et al. (1985b) and Campbell and Taverner (1985), that a steeper linear part in the Pd-curve is associated with a higher plateau. Therefore, in this study a

Table 1. Heritabilities (h^2) on, correlations ($r_p = r_g$) off the diagonal, phenotypic standard deviations (σ_p), common environment components for full sibs (c^2) and economic values (v) used in selection index.

	DG ($g.d^{-1}$)	FIC ($kg.d^{-1}$)	BF (mm)	LP (%)	R	Pd_{max} ($g.d^{-1}$)
Daily gain (DG)	0.3	0.7	0.1	-0.1	-0.5	0.5
Food intake capacity (FIC)	0.7	0.3	0.3	-0.2	0.3	-0.1
Backfat thickness (BF)	0.1	0.3	0.5	-0.6	0.6	-0.6
Percentage lean parts (LP)	-0.1	-0.2	-0.6	0.5	-0.6	0.6
Minimum fat/protein ratio (R)	-0.5	0.3	0.6	-0.6	0.2	-0.4
Maximum protein dep. (Pd_{max})	0.5	-0.1	-0.6	0.6	-0.4	0.2
σ_p	85	0.17	1.5	3.0	0.1	10
c^2	0.15	0.15	0.15	0	0	0
v (if $FIC<FI_o$)1)	-	100	-	-	-70	0
v (if $FIC=FI_o$)	-	2)	-	-	-23	0.8
v (if $FIC>FI_o$)	-	-40	-	-	0	1.0

1) FI_o is the optimum food intake (see Figure 1).

2) Value, depending on level and response of R and Pd_{max}.

correlation of -0.4 was used between R and Pd_{max}. According to Cöp (1974), literature points to correlations of 0.4 to 0.8 between Pd and DG for ad libitum feeding, and somewhat higher correlations for restricted feeding. With ad libitum feeding, probably Pd is often equal to Pd_{max}. With restricted feeding, however, Pd will be highly related to R if $Pd<Pd_{max}$, but this does not necessarily hold for all cases of restricted feeding. In this study, correlations of -0.5 and 0.5 for R and Pd_{max} with DG were assumed. Kanis (1988b) showed that animals with a higher FIC produced more fat and less lean tissue from the same restricted amount of food than animals with a lower FIC. Based on that result, a correlation between R and FIC of 0.3 was assumed. Because of the assumed negative association between R and Pd_{max}, -0.1 was taken for the correlation between FIC and Pd_{max}. Although FIC will have a strong influence on the actual amounts of meat and of fat in the carcass, relatively high correlations of 0.6 between carcass composition traits (BF and LP) and protein deposition traits (R and Pd_{max}) were assumed.

Ranges for R and Pd_{max} are about 0.6 and 60 $g.d^{-1}$, respectively (Whittemore, 1983). Standard deviations for R and Pd_{max} were taken as one sixth of those ranges (Table 1).

Results

In Table 2, expected genetic superiorities (absolute values and units of genetic standard deviation) of the traits are given for index selection with selection differential equal to one standard deviation of the index (i=1). Effects of different economic weights for $FIC<FI_0$ and $FIC>FI_0$ are clearly shown: if $FIC<FI_0$, selection increases FIC and DG, with little change in body composition; if $FIC>FI_0$, selection results in a decrease in FIC, a shift in body composition towards leaner carcasses and a decrease in DG.

For each value of FIC, populations under selection move in the direction of the economic optimum at $FIC=FI_0$ (Figure 1). If $FIC=FI_0$, the selection aim should be to improve the combination of R and Pd_{max}. Change in FIC should be such that the population remains in the economic optimum. In other words, the desired change of FIC depends on the joint improvement of R and Pd_{max}. Economic weights for R and Pd_{max}, under optimal feeding, are now those being de-

Table 2. Expected genetic superiorities (absolute values: abs.[1]; units of genetic standard deviation: rel.) and financial returns (FR), after index selection with selection intensity of 1, for different levels of FIC[2]. See Table 1 for abbreviations.

	$FIC<FI_0$		$FIC>FI_0$		$FIC=FI_0$		Desired gains	
	abs.	rel.	abs.	rel.	abs.	rel.	abs.	rel.
DG ($g.d^{-1}$)	23.5	0.51	-2.2	-0.05	11.4	0.25	19.0	0.41
FIC ($kg.d^{-1}$)	48.7^*	0.52	-36.6^*	-0.39	-9.6	-0.10	5.4^*	0.06
BF (mm)	0.058	-0.06	-0.538	-0.51	-0.527	-0.50	-0.336	-0.32
LP (%)	-0.058	-0.03	0.749	0.35	0.745	0.35	0.477	0.23
R	-3.4^*	-0.08	-26.5	-0.59	-29.6^*	-0.66	-27.7^*	-0.62
Pd_{max} ($g.d^{-1}$)	0.67	0.15	2.18^*	0.49	2.66^*	0.60	2.49^*	0.56
FR (Dfl.)	5.11	-	3.64	-	2.81	-	2.63	-

[1] Absolute superiorities of FIC and R (* 10^3).

[2] Traits with non-zero economic weights in breeding goal are indicated by *.

rived for restricted feeding (-23 and 0.8, see Table 1). Expected genetic superiorities, after selection based on economic values for $FIC=FI_0$, are also given in Table 2. However, if $FIC=FI_0$, the decrease in R and the increase in Pd_{max} must be accompanied by an appropriate change in FIC. According to Figure 1 (assuming M fixed), the desired change in FIC can be calculated. From equation (3) and Figure 1:

$$FI_0 = \frac{Pd_{max}*(1+R)}{243.28} + M \tag{6}$$

If dR and dPd_{max} are the changes in R and Pd_{max}, respectively, the desired change in FIC (dFIC) can be calculated as:

$$dFIC = \frac{dR*Pd_{max} + dPd_{max}*(1+R+dR)}{243.28} \tag{7}$$

Assuming R=1, $Pd_{max}=130$, $dR=-0.0296$ and $dPd_{max}=2.66$ ($FIC=FI_0$ in Table 2), dFIC from (7) is +0.00573, which is a difference of 15.3 $g.d^{-1}$ compared with the value of -0.0096 in Table 2. Results of a desired gains index (Brascamp, 1984) with these changes as relative desired gains are in the last column of Table 2. In fact the change in FIC (0.0054), based on desired gains index, can again deviate from the optimum for $dR=-0.0277$ and $dPd_{max}=2.49$. An iterative procedure would be necessary to find the optimum combination of changes for the three traits. However, the difference between the change in FIC from Table 2 and the optimal change (equation 7) appeared less than 1% and was neglected therefore. The decline in response for R and Pd_{max} with use of the desired gains index, compared with use of the index based on economic values, is only about 6.5% (for R: -0.0277 v. -0.0296, for Pd_{max}: 2.49 v. 2.66). However, due to the increase in FIC, more selection pressure is put on DG, and less on carcass composition. If the increase in FIC must be relatively more, for example if R>1, this tendency becomes more evident (e.g. dFIC= 0.0148 with R=1.5 and $Pd_{max}=100$).

Selection strategy

In the foregoing, short-term selection for lower production costs has been dealt with for certain values of FIC relative to FI_0. If FIC is not equal to FI_0, the optimum FIC can be reached after a number of generations of selection and thereafter a different index should be used. This probably results in a different selection direction with respect to FIC. Such short-term selection is not necessarily optimal economically in the long term. Selection using *a desired gains index* could be *a* method to optimize selection in the long term. To explain this, costs contours were calculated based on the described biological model. Figure 5 shows the corrected production costs per pig with variable R, Pd_{max} and FIC. The costs contours appear to be virtually straight lines. As an example, the effect of FIC on corrected production costs, with R=0.5 and Pd_{max}=200 is represented by line A. If FIC<2.25, then R determines Pd and thus the costs, whereas if FIC>2.25, costs are determined by Pd_{max} (see also Figure 1). With R=1.5 and FIC=2.5 $kg.d^{-1}$, the effect of variation in Pd_{max} is represented by line B (solid part). A protein deposition of more than about 155 $g.d^{-1}$ can not be realized with R=1.5 and FIC=2.5; minimum costs are then about 290 Dfl. per pig. The dotted part of line B represents the effect of R on costs with 0.5<R<1.5, FIC=2.5 and Pd_{max}>240.

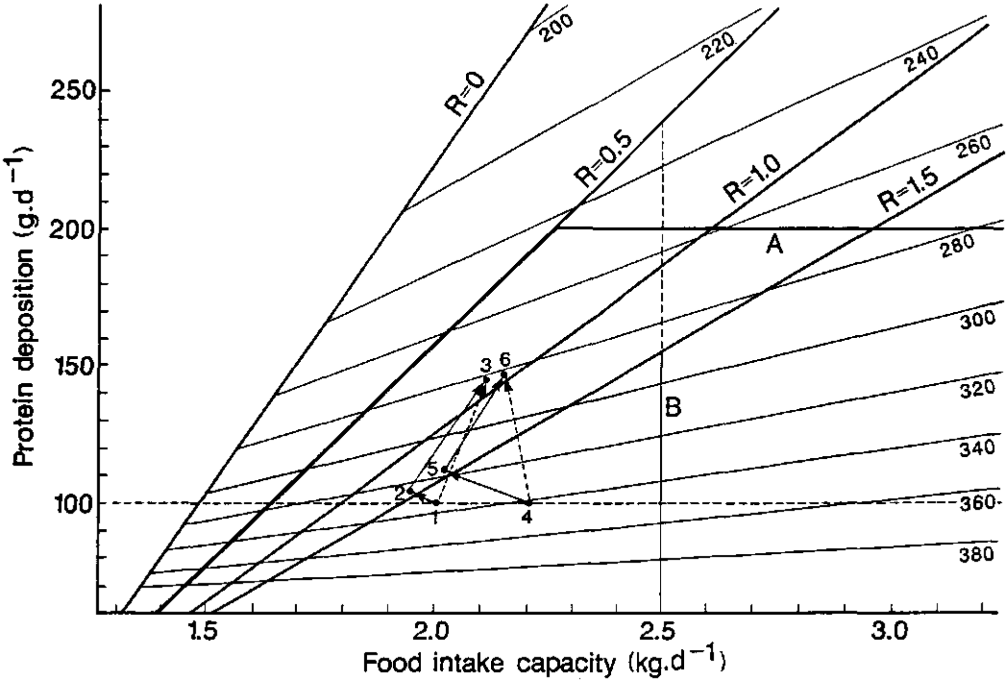


Figure 5. Costs contours (in Dutch guilders per pig) in relation to food intake capacity and protein deposition. See text for explanation.

If $FIC<FI_O$, then short-term selection is concentrated on increasing FIC to realize Pd_{max}. If $FIC=FI_O$, R and Pd_{max} receive more emphasis than if $FIC<FI_O$. Therefore, it could be better to put more weight on R and Pd_{max} before the optimum is reached. However, in each situation ($FIC<FI_O$ and $FIC=FI_O$), selection based on economic values will result in a response in about the same direction. If $FIC<FI_O$, this response is partly caused by a higher Pd, which is possible by the increased FIC. By selection with a desired gains index, total genetic gains are not maximal. So, with discounting of costs, short-term selection is probably not much different from optimal selection in the long term, if the correct indexes are used.

If $FIC>FI_O$, short-term selection results in decreasing FIC (Table 2), whereas the selection direction in the optimum (at $FIC=FI_O$) probably requires an increase of FIC (equation 7). This means that, in the long term it may be better to 'short cut' the decrease and the following increase of FIC with a desired gains index. Figure 5 shows two examples. With selection responses equal to the genetic superiorities given in Table 2, a population in point 1 ($R=1.5$, $Pd_{max}=100$, $FIC=2.0$) will reach point 2 (the optimum) after one generation of selection and point 3 after 20 generations. Cumulative discounted costs are then Dfl. 3780 at an interest rate of 0.05 per generation. By use of a short-cut desired gains index, with the total response of the three traits after 20 generations as relative desired gains, the optimum is reached after somewhat more than 19 generations of selection, with Dfl. 3700 as cumulative discounted costs.

The extra gain of short-cut selection by a desired gains index depends on the distance between initial position of the population and the optimum. Starting from point 4 in Figure 5 ($R=1.5$, $Pd_{max}=100$, $FIC=2.2$), point 5 (the optimum) is reached after five generations of selection and point 6 after 20 generations, with cumulative discounted costs Dfl. 3790. Starting from point 4, point 6 can also be reached after 18 generations of selection based on a short-cut desired gains index, with cumulative discounted costs of Dfl. 3600. Starting from different positions (points 1 and 4) gives about the same result (point 3 and point 6) after 20 generations of selection because of the lower selection response after the optimum is reached. The initial advantage of point 1 is lost due to more generations of selection at $FIC=FI_O$ compared with point 4. Moreover, a relatively high selection response can be achieved in the first generations by selection based on economic values, which is not much affected by the discounting.

Although differences between short-term selection based on economic values and long-term selection by means of a short-cut desired gains index are not large, both examples show that 'short-cut selection' may be worthwhile in the long term. The best selection policy for food intake capacity, apart from genetic and economic parameters, depends on the relative levels of R, Pd_{max} and FIC. If a population, that initially had $FIC > FI_o$, has reached the optimum FIC, it is important to change to the proper selection index. Otherwise, the maximum protein deposition capacity can not be realized because the food intake capacity is too low.

FOOD INTAKE CURVE AND PRODUCTION TRAITS

For simplicity and because of lack of sufficient information on the course of R and Pd_{max} during the growing period, the preceding growth model was based on data, e.g. food intake, averaged over the entire growing period. However, to get a fine tuning of daily food intake on daily R and Pd_{max}, not only the level of average food intake but also the form of the food intake curve may be important. To study this, ad libitum food intake and data on production traits were used from 245 barrows and 32 gilts. Barrows belonged to six batches and gilts to one batch. Feeding, housing and slaughtering procedures of these animals were described by Kanis (1988a).

Ad libitum food intake from 25 to 105 kg live weight was described with the mathematical function (Kanis and Koops, 1988):

$$F = a*e^{-b*W-c/W} \qquad (8)$$

where F = food intake ($kg.d^{-1}$), W = live body weight (kg) and a, b and c are parameters.

To avoid 'atypical' food intake curves, the parameter c was restricted to positive values. For each pig, at 30, 65 and 100 kg live weight, values of the individually predicted functions (F30, F65 and F100) and their first derivatives (tangent; T30, T65 and T100) were calculated. Differences between values (F65-F30, F100-F65, T65-T30 and T100-T65) were also calculated to measure steepness and curvature of food intake curves. Correlations of these characteristics of the food intake curve and of FI with the following production traits defined by Kanis (1988a), were calculated: daily gain (DG), food conversion ratio (FCR), backfat thickness (BF), percentage of lean parts

(LP), percentage of fatty parts (FP), lean tissue growth rate (LTGR), fatty tissue growth rate (FTGR) and lean tissue food conversion (LTFC). Correlations between food intake characteristics and production traits were not much different between batches. Therefore, pooled, within-batch correlations are presented in Table 3.

Table 3. Pooled, within-batch correlations1) between food intake characteristics and production traits with ad libitum feeding (F is predicted food intake and T is tangent of food intake curve at indicated live weights). See text for abbreviations of production traits.

	FI	DG	FCR	BF	LP	FP	LTGR	FTGR	LTFC
FI	1.00	0.73	0.04	0.43	-0.49	0.48	0.44	0.80	0.31
F30	0.06	0.03	0.03	-0.05	0.05	-0.06	0.03	-0.01	0.00
F65	0.88	0.59	0.12	0.42	-0.46	0.47	0.35	0.69	0.31
F100	0.68	0.68	-0.26	0.25	-0.37	0.33	0.40	0.63	0.11
F65-F30	0.58	0.39	0.07	0.32	-0.35	0.37	0.22	0.49	0.22
F100-F65	-0.00	0.25	-0.38	-0.08	-0.01	-0.04	0.14	0.10	-0.14
T30	0.52	0.27	0.18	0.30	-0.30	0.32	0.17	0.39	0.23
T65	0.39	0.50	-0.31	0.15	-0.25	0.21	0.28	0.43	0.01
T100	-0.16	0.11	-0.35	-0.17	0.09	-0.13	0.06	-0.04	-0.19
T65-T30	-0.37	-0.10	-0.27	-0.24	0.20	-0.24	-0.07	-0.23	-0.21
T100-T65	-0.45	-0.19	-0.22	-0.29	0.27	-0.29	-0.11	-0.33	-0.23

1) Absolute values > 0.12 are significantly different from zero ($P<0.05$).

FI appears to be significantly correlated with each production trait, except FCR. Assuming that genetic correlations have the same sign as the presented phenotypic correlations, results confirm that selection for higher growth rates (DG, LTGR, FTGR) would result in an increasing FI. Selection for leaner carcasses (BF, LP, FP) or for lower food conversion ratios (FCR, LTFC) would decrease FI. Predicted food intake at 65 kg and, to a lesser extent, at 100 kg have correlations with production traits similar to correlations of FI with production traits. This was expected because correlations of F65 and F100 with FI are 0.88 and 0.68. F30, however, has no significant correlation with any production trait. Perhaps a low or high food intake in the beginning of the growing period is partly compensated for later. This is confirmed by the correlation of 0.06 between F30 and FI and of -0.17 between F30 and F65.

The correlation of -0.26 between F100 and FCR leads to the conclusion that high food intake capacity at the end of the growing period is associated with favourable food conversion. This seems to be confirmed by the correlations of FCR with F100-F65 (-0.38), T65 (-0.31) and T100 (-0.35), indicating that steadily increasing food intake during the second half of the growing period results in decreasing FCR. However, characteristics of the food intake curve are correlated with FI. Therefore, the standardized partial regression coefficients of production traits on the characteristics of the food intake curve, corrected for FI, are presented in Table 4. It appears that food intake at beginning (F30) and at end (F100) of the growing period is correlated negatively with FCR, whereas the correlation is positive in the middle (F65). This indicates that a straighter food intake curve is favourable for FCR and DG, which is confirmed by the regressions on T65-T30 and T100-T65. A high value for F100 is associated with a high proportion of lean meat in the carcass, and, from the correlations with T65, a steep food intake curve in the middle of the growing period is favourable for body composition. The degree of bending (T65-T30 and T100-T65) seems to be not much associated with body composition. However, the presented characteristics are not independent

Table 4. Standardized partial regression coefficients[1] of production traits on characteristics of the food intake curve, after correction for variation in average daily food intake. (F is predicted food intake and T is tangent of food intake curve at indicated live weights). See text for abbreviations of production traits.

	DG	FCR	BF	LP	FP	LTGR	FTGR	LTFC
F30	0.05	-0.07	0.05	-0.27	0.30	-0.20	0.26	0.19
F65	-0.27	0.40	0.09	0.07	-0.05	-0.07	-0.12	0.05
F100	0.27	-0.41	-0.17	0.25	-0.28	0.31	-0.18	-0.29
F65-F30	-0.10*	0.15	-0.02	0.26	-0.28	0.17	-0.26	-0.16
F100-F65	0.21	-0.32	-0.12*	0.14	-0.16	0.20	-0.09	-0.19
T30	-0.17	0.25	0.06	0.07	-0.08	0.01	-0.11	-0.01
T65	0.16	-0.25	-0.14	0.28	-0.32	0.30	-0.23	-0.30
T100	0.21	-0.32	-0.11*	0.08	-0.10	0.15	-0.04	-0.14
T65-T30	0.19	-0.30	-0.10	0.04	-0.05	0.10	0.01	-0.10
T100-T65	0.18	-0.27	-0.06	-0.09	0.09	0.00	0.12	0.00

[1] Absolute values > 0.12 and those indicated with * are significantly different from zero ($P<0.05$).

and a stepwise approach should be preferred to obtain a clear picture of relationships between the food intake curve and production traits.

Results indicate that animals with a relatively steep food intake curve (but the same FI) have $FIC<FI_0$ (Figure 1) during a longer part of the growing period than animals with a flatter food intake curve. It may be that animals with a high FIC in the beginning of the growing period produce extra fat, which is unfavourable for a further increase of FIC (the correlations of F30 with F65 and with F100 are slightly negative).

By artificially manipulating the food intake curve, similar results may be possible. Wagener (1981) concluded that for barrows (high food intake capacity and high fat producing potential), restricted feeding during the first part of the growing period is commercially interesting. Ad libitum feeding in the second part gave a food conversion ratio that was too high and a slaughter quality that was too low. Donker et al. (1986) showed that restricted feeding in the first half of the growing period, followed by ad libitum feeding, resulted in a lower food conversion ratio, and thicker backfat, than the reverse feeding strategy. Probably ad libitum feeding at the end of the growing period is not optimal for animals with high food intake capacity, as suggested by Donker et al. (1986) and indicated by the unfavourable correlation of F100 with body composition traits in Table 3 (e.g. the correlation between F100 and LP is -0.37). However, a high food intake at the end of the growing period can improve body composition, provided that the total intake is not increased (Table 4).

GENERAL DISCUSSION

Assumptions

In this study, a simple biological growth model was used to elucidate the most desirable selection direction for FIC. As with most models, it is based on several, more or less debatable assumptions. Some of these assumptions will be discussed here.

The linear/plateau relationship between protein deposition and energy intake is mainly based on research of Whittemore and coworkers (Whittemore and Fawcett, 1974; Whittemore, 1983; Morgan and Whittemore, 1986). Gaus (1984) had the view that a quadratic function should be used. A working party of the Agricultural Research Council (ARC, 1981) discussed linear and curvilinear relationships and suggested that the biological truth may lie somewhere in between, depending on strain and sex. However, it is impossible to find the correct relationship for individual animals, because it is not possible to feed an animal on different levels at the same time. Moreover, if FIC<FI_o, Pd_{max} can not be determined at all. In experiments with groups of animals, Campbell et al. (1985b) and Campbell and Taverner (1985) confirmed the linear/plateau relationship for a growing period from 48 to 90 kg live weight. In a study on the relationship between lean tissue growth rate and food intake, during a growing period from 27 to 108 kg, in only two of the seven batches the quadratic component was significant and no clear plateau could be found (Kanis, 1988a). Incorporation of a curvilinear relationship between Pd and FIC is possible, but it needs more complicated (and probably more) parameters than the mathematically simple R and Pd_{max}. These parameters are not available and, moreover, would make it more difficult to explain the problems of selection for FIC. If adequate estimates for R, Pd_{max} and FIC are used, the present simplification will lead to useful conclusions.

Another disputable assumption may be the presumed constancy of daily protein deposition during the entire growing period. This makes it redundant to model daily or weekly changes in protein deposition or body composition to calculate averages over the growing period. In fact, the requirement is not so severe as it looks. For instance, increasing Pd in the first half of the growing period, followed by similar decreasing Pd in the second half, gives the same $\bar{E}_m$ (equation 2) as a constant average Pd. Such symmetry around the median live weight has been demonstrated for protein deposition between 25 and 105 kg live weight (Tullis, 1981; Siebrits et al., 1985).

For simulation of selection effects, phenotypic and genetic parameters of index and breeding goal traits are needed. These can be quite different for restricted and ad libitum feeding (e.g. Standal and Vangen, 1985). It is likely that parameters can also be different for populations with different values of FIC compared with FI_o (Figure 1). This is illustrated for some phenotypic relationships in Figure 2. However, appropriate values are not available so that one parameter set was chosen, which was assumed to hold for populations with an average FI around FI_o. For more detailed insight into the usefulness of the model for selection purposes, different alternative parameter sets should be taken. The advantage of the present approach is that the effect of different economic values is not confounded with different sets of parameters. It is evident that for practical use, parameters should be taken from the populations in question. Despite the many uncertain parameters in this study, the expected genetic superiorities (Table 2) reflect what is often observed in practice. The assumed unfavourable correlations of R and Pd_{max} with FIC are rather critical in this respect. Presuming that most of the western strains of pigs under ad libitum feeding have, or had, $FIC>FI_0$ during the major part of the growing period, by selection for higher meat percentage and higher food efficiency, and little selection weight on daily gain, they move quite rapidly to a situation of $FIC=FI_0$. It may well be that boars of some lean strains already have a food intake capacity that is not sufficient to realize Pd_{max} (Campbell and Taverner, 1985). To realize maximum profit, it is important then to use the selection index based on the correct economic values.

Future selection strategy

Literature indicates that index selection with much weight on carcass leanness and food efficiency will result in little or no change in DG, but FIC will decline (see review by Vangen and Kolstad, 1986). With sufficient selection emphasis on DG, deterioration of FIC can be avoided (Vangen, 1980; Ollivier, 1986). From selection in broilers, for example, it is known that single trait selection for body weight at a fixed age, results in fat animals with a high FIC (Leenstra, 1987). The key to selection for production traits apparently is to find the optimum balance between selection for carcass quality, growth rate and food intake. As suggested also by Webb (1986), the selection index that may be optimal in the short term is not always in line with the biological optimum in the long term. The consequence may be that the response (or lack of response) in FIC limits the response in LTGR. In a simulation study (R. Hovenier, N. Buddiger and R. Eek, unpublished results), it was assumed that, by application of index selection based on economic weights, average FIC in a population moves from $FIC>FI_0$ to $FIC=FI_0$ or to $FIC<FI_0$, and that the phenotypic variation in LP caused by variation in FIC decreases (Figure 2b). After some generations of selection, it appeared that selection emphasis changed from LP to DG because variation in DG caused by variation in FIC was not reduced at $FIC=FI_0$ or at $FIC<FI_0$ (Figure 2a). Because of the positive correlation between DG and FIC, FIC increased again. This is not the optimal way to select, but it illustrates that the population moves eventually in the desired direction, even with a sub-optimal selection index.

Results in Table 2 show that different economic weights in the breeding goal can lead to different selection directions. For optimal selection results, correct economic values or relative desired gains are important. These depend largely on the actual genotypic levels of R, Pd_{max} and FIC, which are considered as driving variables for pig meat production. Restricting FIC to zero response or putting a higher economic weight on daily gain, without regard to levels of R, Pd_{max} and FIC, may be pragmatic and sub-optimal measures to prevent further decrease of FIC. Research to obtain more information on levels and phenotypic and genetic parameters of R, Pd_{max} and FIC, in combination with other relevant production and reproduction traits should be stimulated.

It may be expected that in the long run, R becomes less important as a breeding goal trait, due to reaching a biological limit, because protein deposition must always be accompanied by some minimum fat deposition. Moreover, it is likely that a minimum amount of fat in the carcass is necessary to guarantee sufficient meat quality. With respect to meat quality, it can be imagined that the optimum with low values of R is not even at $FIC=FI_o$ in Figure 1, but somewhere to the right. In that case, selection should be for Pd_{max} and FIC, and not for R.

Because FIC appears to be, or will become an important trait to select for, testing of breeding stock should be done with ad libitum feeding. For a practical commercial farmer, it may well be optimal to feed according to scale if pigs have a $FIC>FI_o$. Genotype by feeding regimen interaction may then occur. For example, suppose that selection is carried out with the selection index for $FIC>FI_o$ in Table 2. An animal with a sufficient R and Pd_{max} may not be selected because of a high degree of fatness due to a high FIC. However, for restricted feeding this animal would be a good one. Relationships between Pd and FI may be different among commercial farms (e.g. herd effects on R or Pd_{max}). This may cause genotype by environment interaction. Merks (1988) suggests, therefore, to select breeding boars on the basis of half-sib or progeny information from the commercial farms. The breeding goal is then defined for the average commercial environment. As an alternative, it would also be possible, in principle, to classify farms on the basis of their average R and Pd_{max}, or related traits, and to define FI_o for each class of farms. For performance tested boars, levels of index traits could be calculated at each FI_o by means of a biological growth model. Selection indices for restricted feeding for each class of farms could then be derived, even with testing under ad libitum feeding.

If selection is mainly for Pd_{max}, optimum food intake will increase. Therefore, it is likely that in the future the optimum feeding strategy is ad libitum or almost ad libitum feeding, even on commercial farms. From a breeding point of view, this is an advantage because genotype by environment interaction (for test-station compared with practical circumstances) will diminish if genotype by feeding regimen interaction disappears (Kanis, 1988c).

An implicit assumption in the model was that all animals use the food with equal efficiencies for maintenance, protein and fat deposition. Waste of food, differences in maintenance requirements, activity, or other possible sources of residual food intake were not taken into account. Research in pigs (Foster et al., 1983) and laying hens (Luiting and Urff, 1987) indicates that residual FI is variable and heritable. It is possible to incorporate residual FI into the growth model and the breeding goal by modifying $\bar{E}_m$ (equation 2). The graphical consequences of a variable residual FI are that M is a variable (Figure 1) and that the position of the lines for R and the costs contours depend on the value of M (Figure 5). Luiting and Urff (1987) suggested that selection for lower residual FI could avoid a possible drawback in response for production traits because of reduced appetite. However, if $FIC>FI_0$, selection for a lower residual FI means that FI_0 will decrease, and that it will be reached later and at lower costs. In the long term, genetic response from decreasing residual FI is expected to be limited and the major return should come from increasing Pd_{max}, accompanied by the appropriate increase in FIC.

Kalm and Krieter (1985) and Krieter (1986) found that daily food intake in the beginning of the growing period had less unfavourable genetic correlations with LP and more favourable correlations with LTGR than daily food intake over the entire growing period. This may be an indication that, in young animals, $FIC<FI_0$ because then FI affects DG, but not LP (Figures 2a and 2b). Also Campbell et al. (1985a) found a linear relationship between FI and Pd in pigs growing from 20 to 45 kg live weight. If $FIC<FI_0$ during part of the growing period, it might be worthwhile to put more selection emphasis on that part of the food intake curve to keep step with the maximum protein deposition. The present study indicates that it might be useful to give more emphasis to the food intake at the end of the growing period. The advantage of increasing food intake at the beginning of the growing period (with equal total FI) could not be confirmed (Table 4). This may be due to the high food intake compared with other studies.

In many western pig breeds, during the last decades, financial returns from selection have been based heavily on improvement of body composition and reduction in food costs (selection based on short term economic values with $FIC>FI_0$). If the optimum combination of protein deposition and FIC has been reached, future selection is less profitable than before the optimum. For example, a difference in financial returns of 27.8% was found between index selection if $FIC>FI_0$ and selection with a desired gains index in the optimum (Table 2). Deterioration of future selection returns from production traits makes selection for other traits, such as reproduction and conformation, relatively more important.

Results show that optimal testing and selection of growing pigs requires knowledge of the biology of the pig, in combination with the market conditions. More information is needed about the genetic background of protein deposition. In the future, it will no longer be sufficient to record only 'external' traits, such as average daily gain and backfat thickness at the end of the test. Recent developments in measuring body composition of live animals by ultra-sound (Molenaar, 1985), X-ray (Allen, 1985) or NMR scanners (Groeneveld et al., 1984) may result in useful tools in pig breeding. To determine the levels of R and Pd_{max} necessary for calculation of economic weights, nitrogen balance could become part of testing procedures. For optimal results in practice, fine tuning of feeding strategy on the genotype of growing pigs is necessary.

ACKNOWLEDGEMENT

The pilot simulations carried out by Nico Buddiger, Ron Eek, Ron Hovenier, Hans Leneman, Antoon van Bommel and Gerrit van Heijst and the discussions with them are gratefully acknowledged.

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SUMMARY

The production of an animal depends on its genotype and its environment. Therefore, in general, two ways exist to improve production traits: improvement of the genotype and improvement of the environment. In growing pigs, the first is often done by selection for a combination of economically important traits, such as average daily growth rate, food conversion ratio and proportion of lean meat in the carcass. The amount of food offered to a pig can be considered a major environmental factor, particularly with restricted feeding. With ad libitum feeding, food intake is assumed to be equal to food intake capacity, which contains a genetic component. High food intake may result in unfavourable food conversion ratio and high proportion of fat in the carcass. Therefore, growing pigs are often fed at a restricted feeding level during part of the growing period.

There is evidence that selection programmes giving high emphasis to food conversion ratio and lean proportion, at the expense of growth, can lead to reduction in food intake capacity, especially with testing under ad libitum feeding. However, a low food intake capacity can become a constraint for further improvement of body-weight gain and lean tissue growth rate.

In this thesis, relationships of food intake and food intake capacity with production traits were studied. Implications of variation in food intake capacity for breeding and feeding strategies were discussed. Production traits dealt with were: average daily body weight gain (DG), food conversion ratio (FCR), ultrasonically measured backfat thickness (BF), percentage lean parts in the carcass, percentage fatty parts in the carcass, lean tissue growth rate (LTGR), fatty tissue growth rate (FTGR) and lean tissue food conversion (LTFC).

Results were based on a series of six experiments with growing pigs, fed according to different strategies. For each experiment, a fixed number of animals per litter (Dutch Yorkshire * Dutch Landrace crossbreds) was purchased. Animals were housed and fed individually. On a total of 687 barrows (experiments 1 to 6) and 98 gilts (only in experiment 6), live body weight and food intake were recorded weekly during a growing period from about 27 to 108 kg live weight. At the end of the growing period, backfat thickness was measured ultrasonically. Carcasses were dissected and amounts of lean and fatty tissue in the carcasses were determined.

In chapter 1, relationships of average daily food intake (FI) with production traits were investigated for each experiment by sex combination. Because animals were fed on different feeding levels, FI ranged from about 1.7 $kg.d^{-1}$ to 3.2 $kg.d^{-1}$ (22 to 42 MJ digestible energy per day). Body composition appeared to be linearly related to FI, showing fatter animals at higher FI. FTGR had a high linear correlation with FI (0.85 to 0.95), indicating that in the present range of FI a rather fixed proportion of food for production was used to deposit fatty tissue. The response of DG and of LTGR on increasing FI was not always significantly different from linear. However, quadratic polynomials indicated diminishing returns in each experiment. Therefore, a non-linear regression model of the type $a(FI-f_0)^b$, with parameters a, f_0 and b, was fitted to the data on DG and LTGR. For FCR and LTFC the corresponding model was: $FI/(a(FI-f_0)^b)$. These non-linear models were preferred over quadratic polynomials because of good fit and better biologically interpretable parameters.

FCR and LTFC showed minima at a daily food intake of about 2.6 and 2.2 kg per day, respectively. At a high feeding level, the increase of FCR with increasing FI was low. Compared to most literature, the minimum FCR was at higher FI. Results were not consistent in demonstrating or refuting a plateau in LTGR, which, in any event, appears to lie near to or beyond ad libitum FI for most pigs.

In each experiment, each animal had two to five littermates of the same sex. In each litter, one to three animals were fed ad libitum and two or three were fed at a restricted feeding level. In experiments 1 to 5, animals fed at a restricted feeding level received a constant proportion of ad libitum intake of animals in the same experiment at similar weight. In experiments 6 and 7, animals on restricted feeding were fed ad libitum to 48 kg live weight and according to scale afterwards. Food intake capacity (FIC) of animals fed at a restricted feeding level was estimated by two methods. The first method consisted of assigning the average daily food intake of ad libitum fed littermates of the same sex to each animal fed at a restricted feeding level. The second method could only be applied to experiment 6. It consisted of estimating FIC with multiple regression based on individual ad libitum performance till 48 kg live weight.

Effect of FIC on production traits was discussed in chapter 2. It was shown that FIC had a significant effect on body composition traits but not on DG and FCR. Irrespective of the method used to estimate FIC, animals with higher FIC produced more fatty tissue and less lean tissue from the same amount of food than animals with lower FIC. It was suggested that the partition of metabolizable energy between energy for maintenance, protein deposition and fat deposition is associated with FIC. The findings confirmed that selection for leaner and more efficient pigs may result in animals with lower FIC, irrespective of the feeding strategy during performance testing.

From recent literature, it is known that estimated genetic correlations of production traits (especially growth) measured in test-stations with similar traits measured in commercial environments, are lower than expected. This type of genotype by environment interaction has a negative influence on efficiency of breeding programmes because the breeding goal is generally defined in the commercial environment. Variation in degree of food intake restriction (DFR) may be a possible reason for these interactions because often in one or even in both environments, restricted feeding is applied according to scale. This means that animals receive an amount of food irrespective of their FIC and thus variation in DFR occurs.

In chapter 3 this hypothesis was tested by investigating the effect of DFR on litter by feeding regimen (L*F) interaction in animals fed at a restricted feeding level. It appeared that L*F interactions were significant for FI, DG, LTGR and FTGR in experiments 4 and 5. In experiment 6, sex by feeding regimen (S*F) interactions were significant for the same traits. L*F or S*F interactions were not significant for body composition and food conversion traits. Experiments 4 to 6 were also the experiments where not all animals received food according to their FIC. Correction of FI and production traits for differences in DFR resulted in disappearance of L*F and S*F interactions. It was concluded, therefore, that the poor relationships often found between test-station results of boars and results of their progeny in commercial environments may be caused, to a large extent, by variation in DFR in one or both environments. The easiest way to prevent these genotype by environment interactions is to feed animals ad libitum in test and in commercial environments.

In chapter 4, courses of daily gain, food intake and food efficiency (FE, defined as daily gain over food intake) during the normal growing period were described. Knowledge of these courses is necessary to optimize feeding strategies. The non-linear model $y=a*\exp(-b*W-c/W)$ was fitted to weekly recorded DG, FI and FE of 653 barrows and gilts fed at ad libitum or restricted feeding levels. In this model, y is DG, FI or FE, W is live body weight and a, b and c are parameters. The model had attractive mathematical properties and fitted well to the expected course of the traits investigated. The accuracy was similar to that of quadratic polynomials. Coefficients of determination in barrows averaged 0.29 for DG, 0.88 for FI and 0.45 for FE. In gilts these values were somewhat lower. For each trait, four types of curves could be distinguished, depending on the signs of b and c. With ad libitum feeding, 83% of the barrows and 61% of the gilts had a curve for DG with a maximum (b and c both positive). The predicted maximum DG was at an average live weight of 64 kg for barrows and 77 kg for gilts. In 60% of the barrows and 39% of the gilts, a FI curve with a maximum was found. Curves for DG and FI in gilts were flatter than in barrows. FE curves had a maximum in 59% of the barrows and in 52% of the gilts fed ad libitum. This predicted maximum FE, however, was, on average, before the start of the growing period. With ad libitum feeding, gilts had a higher FE than barrows from 35 kg body weight onwards. The difference between gilts and barrows increased with increasing live weight. Differences in FE between pigs fed ad libitum and pigs fed at restricted feeding levels were small, with a tendency for restrictedly fed pigs to be more efficient at the end of the growing period.

For each combination of experiment, feeding level and sex, average FE curves and individual FI or DG curves were used for indirect prediction of individual DG or FI curves, respectively. The correlation between directly and indirectly predicted values of DG and of FI at different weights was about 0.7 in ad libitum fed barrows and gilts, and over 0.8 in pigs fed at a restricted level. This indicates that the model is suitable to predict and control the course of individual daily gain of growing pigs by influencing the course of food intake.

In the literature, some pragmatic solutions are given to prevent further decline of FIC, such as more selection emphasis on DG or restriction of the genetic change of FIC to zero. In chapter 5, a method is presented to optimize selection for FIC by means of a biological growth model based on the linear/plateau relationship between protein deposition and food intake. Production costs were calculated with input variables: minimum fat to protein deposition ratio (R), maximum protein deposition rate (Pd_{max}) and FI. Economic values were estimated for breeding goal traits R, Pd_{max} and FIC at three alternative levels of FIC. If FIC was too low to realize Pd_{max}, the economic value of FIC was about 100 Dfl. per $kg.d^{-1}$ and optimal selection emphasis should be mainly on FIC, resulting in a rapid increase of daily weight gain. If FIC was higher than necessary to realize Pd_{max}, the economic value of FIC was about -40 Dfl. per $kg.d^{-1}$ and short-term selection resulted in increase of carcass leanness but decrease of FIC and DG. If FIC was just sufficient to realize Pd_{max}, the lowest production costs occurred and selection should be for R and Pd_{max}. In this third alternative, the gain in FIC should follow the gain in R and Pd_{max} in an optimal way and selection should best be carried out with a desired gains index, which will result in improvement of DG and of carcass leanness. It was shown that, in cases where FIC was higher than necessary to realize Pd_{max}, selection with a desired gains index should be preferred because this is more profitable in the long term. From the model calculations, it followed that future profit from selection of growing pigs for production traits is likely to decline because of the necessity to increase food intake capacity.

In the second part of chapter 5, the relationship between the shape of the food intake curve and production traits was investigated. After correction for variation in average daily FI, more curvature of the food intake curve appeared to be associated with a lower DG and a higher food conversion ratio. A high food intake at the end of the growing period (with the same FI) was favourable for DG and for carcass leanness.

To achieve optimal results in pig meat production, accurate tuning of selection procedures and feeding regimens on the biological possibilities of the pig will be required. More knowledge is necessary concerning the genetic background of protein deposition and lean tissue growth in pigs.

SAMENVATTING

De produktie van een dier wordt bepaald door zijn erfelijke aanleg en door het milieu waarin het zich bevindt. In het algemeen zijn er dus twee mogelijkheden om de produktie per dier te verhogen, namelijk verbetering van de erfelijke aanleg en verbetering van het milieu. Bij vleesvarkens tracht men het eerste meestal te bereiken via selectie op een combinatie van economisch belangrijke kenmerken zoals groei, voederconversie en vleespercentage in het karkas. Er zijn vrij duidelijke aanwijzingen dat selectieprogramma's waarin veel nadruk wordt gelegd op voederconversie en vleespercentage en weinig op groei, kunnen resulteren in varkens met een verlaagd voeropnamevermogen, vooral bij selectie in een ad libitum voedersysteem.

De hoeveelheid voer die een varken aangeboden krijgt kan worden beschouwd als een belangrijke milieufactor, vooral bij een beperkt voersysteem. Bij ad libitum voeren kan de voeropname gelijk worden gesteld aan het voeropnamevermogen en dat is gedeeltelijk erfelijk bepaald. Een hoge voeropname kan leiden tot een ongunstige voederconversie en veel vet in het karkas. Dat is de reden waarom vleesvarkens vaak beperkt worden gevoerd gedurende een deel van de mestperiode. Als echter door de toegepaste selectiemethode het voeropnamevermogen daalt (of te weinig stijgt) kan dit een beperking worden voor de verdere verbetering van de vleesgroei.

Dit proefschrift heeft betrekking op de verbanden van voeropname en voeropnamevermogen met produktiekenmerken en op de betekenis van deze verbanden voor de varkensfokkerij. De bevindingen zijn gebaseerd op een serie van zes proeven met vleesvarkens die volgens verschillende strategieën werden gevoerd. Voor elke proef werd een van tevoren vastgesteld aantal dieren per toom aangekocht van het kruisingstype Groot Yorkshire * Nederlands Landras. Alle dieren werden individueel gehuisvest en gevoerd. Van in totaal 687 borgen (in proef 1 tot en met 6) en 98 gelten (alleen in proef 6) werd wekelijks het levend gewicht en de voeropname bepaald gedurende een mestperiode van ongeveer 27 tot 108 kg. Aan het eind van de mestperiode werd de spekdikte ultrasonisch gemeten. Na het slachten werden alle karkassen uitgesneden en werd de hoeveelheid vleesrijke en vetrijke delen bepaald.

In hoofdstuk 1 is voor elke combinatie van geslacht en proef het verband beschreven tussen de gemiddelde dagelijkse voeropname en de volgende produktiekenmerken: gemiddelde dagelijkse groei, voederconversie, ultrasonisch gemeten spekdikte, percentage vleesrijke delen in het karkas, percentage vetrijke delen in het karkas, vleesgroei, vetgroei en vleesvoederconversie. Doordat verschillende voerniveaus werden gehanteerd, varieerde de gemiddelde voeropname van ongeveer 1,7 tot 3,2 kg per dag (22 tot 42 MJ verteerbare energie per dag).

Het verband tussen voeropname en lichaamssamenstelling bleek niet significant af te wijken van lineair. Een hogere voeropname ging daarbij samen met meer vet en minder vlees in het karkas. De lineaire correlatie tussen voeropname en vetgroei was erg hoog (0,85 tot 0,95), hetgeen aangeeft dat binnen het traject waarop de voeropname onderzocht is, een tamelijk vaste fractie van het voor de groei beschikbare voer wordt besteed aan vetaanzet.

Het verband van voeropname met groei en met vleesgroei verschilde niet altijd significant van lineair. Kwadratische polynomen lieten echter in alle proeven een "afnemende-meeropbrengst-verloop" zien. Naar aanleiding hiervan werd onderzocht of met een niet-lineaire regressie-vergelijking van het type $a(FI-f_0)^b$, waarbij a, f_0 en b de parameters zijn en FI de voeropname, een goede beschrijving van het verband van voeropname met groei en vleesgroei kon worden verkregen. Voor voederconversie en vleesvoederconversie was het corresponderende model: $FI/(a(FI-f_0)^b)$. Er werd vastgesteld dat beide niet-lineaire modellen de voorkeur verdienen boven kwadratische polynomen omdat hun parameters beter biologisch te interpreteren zijn. Voederconversie en vleesvoederconversie vertoonden meestal een minimum bij een voeropname van respectievelijk ongeveer 2,6 en 2,2 kg/dag, maar vooral voor voederconversie gold dat de toename bij hogere voeropname gering was. De minimale voederconversie lag bij een hogere voeropname dan in de meeste literatuur wordt vermeld. De resultaten waren niet eenduidig met betrekking tot het aantonen van een bereikt of te bereiken plateau voor vleesgroei bij hogere voeropnamen.

In alle proeven had elk dier een tot vijf toomgenoten van dezelfde sexe. In elke toom werden een of meer dieren ad libitum gevoerd en twee of meer beperkt. In de proeven 1 tot en met 5 kregen de beperkt gevoerde dieren een vaste fractie van de ad libitum voeropname van bepaalde dieren bij hetzelfde gewicht in dezelfde proef. In proef 6 zijn de beperkt gevoerde dieren eerst ad libitum gevoerd tot zij een gewicht van 48 kg hadden bereikt en daarna beperkt gevoerd volgens een vast schema. Van de beperkt gevoerde dieren werd het voeropnamevermogen geschat volgens twee methoden. De eerste methode hield in dat het voeropnamevermogen gelijk werd gesteld aan de gemiddelde voeropname van alle ad libitum gevoerde toomgenoten van hetzelfde geslacht. Bij de tweede methode werd het voeropnamevermogen geschat via multipele regressie uit de individuele resultaten bij ad libitum voedering tot 48 kg. Deze methode kon alleen worden toegepast in proef 6.

Het effect van voeropnamevermogen (gecorrigeerd voor verschillen in werkelijke voeropname) op produktiekenmerken is beschreven in hoofdstuk 2. Voeropnamevermogen had een significant effect op lichaamssamenstelling, maar niet op groei en voederconversie. Ongeacht de gebruikte methode om voeropnamevermogen te schatten, bleek dat dieren met een hoger voeropnamevermogen meer vet en minder vlees aanzetten uit dezelfde hoeveelheid voer dan dieren met een lager voeropnamevermogen. Dit zou kunnen betekenen dat de verdeling van de beschikbare energie over onderhoud, vleesaanzet en aanzet van vetweefsel samenhangt met het voeropnamevermogen. De resultaten ondersteunen de theorie dat selectie van vleesrijkere en efficiëntere varkens kan leiden tot dieren met een lager voeropnamevermogen, ongeacht of de selectie plaats vindt bij een ad libitum of een beperkt voersysteem.

Uit recente literatuur is bekend dat geschatte genetische correlaties tussen enerzijds produktiekenmerken (met name groei) gemeten op toetsstations en anderzijds vergelijkbare kenmerken gemeten op praktijkbedrijven lager zijn dan verwacht. Deze vorm van genotype-milieu interactie heeft een negatieve invloed op de effectiviteit van fokprogramma's, omdat het fokdoel in het algemeen op praktijkniveau gedefinieerd is. Verschillen in de mate van voerbeperking zouden een mogelijke verklaring voor deze interactie kunnen zijn, omdat vaak in een of zelfs in beide milieus beperkte voedering volgens een bepaald schema wordt toegepast. Dit brengt met zich mee dat beperkt gevoerde dieren een hoeveelheid voer krijgen zonder dat rekening gehouden wordt met hun opnamevermogen, zodat dus variatie in de mate van voerbeperking ontstaat.

In hoofdstuk 3 is bovenstaande hypothese getoetst door te onderzoeken wat het effect is van de mate van voerbeperking op de interacties tussen toom en voerregime (ad libitum of beperkte voedering). Alleen in de proeven 4 en 5 bleken deze interacties significant te zijn voor de kenmerken voeropname, groei en vleesgroei. In proef 6 waren interacties tussen geslacht en voerregime significant voor dezelfde kenmerken. Voor kenmerken betreffende voederconversie of lichaamssamenstelling werden geen significante interacties gevonden tussen toom en voerregime of tussen geslacht en voerregime. De proeven 4 tot en met 6 waren tevens de proeven waarin niet alle dieren volgens hun voeropnamevermogen werden gevoerd. Na correctie van voeropname en produktiekenmerken voor verschillen in de mate van voerbeperking bleken noch de interacties tussen toom en voerregime, noch die tussen geslacht en voerregime meer significant. Er werd daarom geconcludeerd dat het slechte verband dat vaak gevonden wordt tussen de resultaten op toetsstations en die in de praktijk, in belangrijke mate toegeschreven kan worden aan variatie in de mate van voerbeperking in een of beide milieus. De gemakkelijkste manier om deze genotype-milieu interacties te voorkomen is ad libitum te voeren onder zowel toets- als praktijkomstandigheden.

In hoofdstuk 4 is het verloop van dagelijkse groei, voeropname en voederefficientie tijdens de mestperiode onderzocht. Kennis hieromtrent is nodig om te komen tot optimalisering van voederstrategieën. Het niet-lineaire regressie-model $y=a*e^{(-b*W-c/W)}$ werd gebruikt om de wekelijks verzamelde gegevens aangaande groei, voeropname en voederefficiëntie te beschrijven van 653 ad libitum en beperkt gevoerde borgen en gelten. In dit model kan y staan voor groei, voeropname of voederefficiëntie. W is levend gewicht, e is het grondtal van de natuurlijke logaritme, terwijl a, b en c de parameters zijn. Het model had aantrekkelijke mathematische eigenschappen en sloot goed aan bij het verwachte verloop van de onderzochte kenmerken. De nauwkeurigheid was vergelijkbaar met die van kwadratische polynomen. Gemiddeld bedroeg de fractie van de individuele variantie die door het model kon worden verklaard 0,29, 0,88 en 0,45 voor respectievelijk groei, voeropname en voederefficiëntie van de borgen. Voor de gelten waren deze waarden iets lager. Voor elk kenmerk werden vier typen curven onderscheiden, afhankelijk van het teken van de parameters b en c. Bij ad libitum voedering vertoonde 83% van de borgen en 61% van de gelten een groeicurve met een maximum (b en c beide positief). Dit maximum werd bereikt op een gemiddeld gewicht van respectievelijk 64 en 77 kg. Bij 60% van de borgen en 39% van de gelten werd een maximum in de voeropnamecurve gevonden. De groei- en voeropnamecurven van de gelten vertoonden een vlakker verloop dan die van de borgen. De voederefficiëntiecurven vertoonden een maximum bij 59% van de ad libitum gevoerde borgen en bij 52% van de ad libitum gevoerde gelten. Deze maximale voederefficiëntie (indien aanwezig) trad echter al op voor het begin van de mestperiode. Vanaf 35 kg hadden gelten een hogere voederefficiëntie dan borgen en dit verschil werd groter met toenemend gewicht. Verschillen in voederefficiëntie tussen ad libitum en beperkt gevoerde varkens waren klein met een tendens dat beperkte voedering iets efficiënter was aan het eind van de mestperiode.

Om indirect het verloop van groei of voeropname te voorspellen op basis van gewenste individuele curven voor respectievelijk voeropname en groei, zijn gemiddelde voederefficiëntiecurven per combinatie van proef, voerniveau en geslacht gebruikt. De correlatie tussen direct en indirect geschatte waarden voor groei en voeropname bleek bij verschillende gewichten ongeveer 0,7 te zijn voor ad libitum gevoerde dieren. Voor beperkt gevoerde dieren was deze zelfs iets hoger. Dit geeft aan dat het model zich leent om het verloop van de individuele groei van varkens te voorspellen en te besturen via het voeropnameverloop.

Om verdere teruggang van voeropnamevermogen te voorkomen worden in de literatuur enkele pragmatische oplossingen voorgesteld, zoals meer selectiedruk op groei of een zogenaamde nulrestrictie op voeropnamevermogen. In hoofdstuk 5 is een methode beschreven om selectie op voeropnamevermogen te optimaliseren met behulp van een biologisch groeimodel dat gebaseerd is op het "lineair/plateau model" voor de relatie tussen eiwitaanzet en voeropname. Met als inputvariabelen minimale vet-/eiwitaanzet verhouding, maximaal mogelijke eiwitaanzet en voeropname werden produktiekosten berekend. Hieruit volgden economische waarden voor de minimale vet-/eiwitaanzet verhouding, de maximale eiwitaanzet en het voeropnamevermogen als fokdoelkenmerken, bij drie alternatieve niveaus van voeropnamevermogen. Als het voeropnamevermogen te laag was om de maximale eiwitaanzet te kunnen realiseren was de economische waarde voor voeropnamevermogen ongeveer 100 gulden per kg/dag. De selectiedruk diende dan vooral te liggen op voeropnamevermogen. Dit resulteerde in een snelle toename van de groei. Als het voeropnamevermogen ruimschoots voldoende was om de maximale eiwitaanzet te realiseren was de economische waarde van voeropnamevermogen ongeveer -40 gulden per kg/dag. Optimale selectie (op korte termijn) resulteerde dan in een verhoging van het vleespercentage in het karkas en een teruggang van het voeropnamevermogen en de groei. Als het voeropnamevermogen juist voldoende was om de maximale eiwitaanzet te realiseren werden de laagste produktiekosten bereikt. De selectie moest dan gericht worden op verbetering van de minimale vet-/eiwitaanzet verhouding en de maximale eiwitaanzet, waarbij voeropnamevermogen zodanig moest veranderen dat steeds de optimale situatie gehandhaafd bleef. Dit kon het beste gedaan worden via selectie met een selectie-index gebaseerd op gewenste erfelijke vooruitgangen (desired gains index) in plaats van op economische waarden. Dit resulteerde in verbetering van groei en vleespercentage. Het bleek dat, ook als het voeropnamevermogen (ruimschoots) voldoende was om de maximale eiwitaanzet te realiseren, een dergelijke index de voorkeur verdiende omdat daarmee op de langere termijn meer winst behaald kon worden.

Uit de modelberekeningen kon worden afgeleid dat de toekomstige winstgevendheid van selectie op produktiekenmerken bij vleesvarkens waarschijnlijk zal afnemen. Dit wordt veroorzaakt door de noodzaak het voeropnamevermogen te verhogen.

In het tweede deel van hoofdstuk 5 werd ingegaan op de relatie tussen de vorm van de ad libitum voeropnamecurve en produktiekenmerken. Na correctie voor verschillen in gemiddelde voeropname per dag bleek dat meer buiging van de voeropnamecurve samenging met een lagere groei en een hogere voederconversie. Een hoge voeropname aan het eind van de mestperiode (bij dezelfde gemiddelde voeropname) was gunstig voor de groei en het vleespercentage in het karkas.

Om in de toekomstige varkensvleesproduktie optimale resultaten te bereiken, is een nauwkeurige afstemming van selectieprocedures en voederstrategieën op de biologische mogelijkheden van het varken vereist. Daartoe is meer kennis nodig omtrent de genetische achtergronden van eiwitgroei en vleesgroei bij varkens.

Curriculum vitae

Egbert Kanis werd op 22 september 1953 geboren in Zalk (gemeente IJsselmuiden) en is getogen op een melkveebedrijf in Ens (Noordoostpolder). In 1971 behaalde hij het diploma HBS-B aan het Prof. Ter Veenlyceum in Emmeloord. In datzelfde jaar begon hij met de studie Zoötechniek aan de toenmalige Landbouwhogeschool te Wageningen. Het doctoraalexamen werd afgelegd in 1977 met als hoofdvak de Veeteelt, als bijvakken de Gezondheids- en Ziekteleer der Huisdieren, de Erfelijkheidsleer en de Veevoeding, en als extra bijvak de Visteelt en Visserij. Na zijn afstuderen werd hij aangesteld als wetenschappelijk medewerker en later als universitair docent bij de vakgroep Veefokkerij van de huidige Landbouwuniversiteit.