RELEVANCE OF EATING PATTERN FOR SELECTION OF GROWING PIGS

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in het bijzonder de voeding van de eenmagigen

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Proefschrift

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De Haer, L.C.M., 1992. Relevance of eating pattern for selection of growing pigs (Belang van het voeropnamepatroon voor de selektie van groeiende varkens). In this thesis investigations were directed at the consequences of testing future breeding pigs in group housing, with individual feed intake recording. Subjects to be addressed were: the effect of housing system on feed intake pattern and performance, relationships between feed intake pattern and performance and genetic aspects of the feed intake pattern. Housing system significantly influenced feed intake pattern, digestibility of feed, growth rate and feed conversion. Through effects on level of activity and digestibility, frequency of eating and daily eating time were negatively related with efficiency of production. Meal size and rate of feed intake were positively related with growth rate and backfat thickness. Feed intake traits had moderate heritabilities. Doctoral Thesis, Research Institute for Animal Production (IVO-DLO) 'Schoonoord', P.O. Box 501, 3700 AM Zeist, The Netherlands. Present address: V.O.C. Nieuw-Dalland B.V., P.O. Box 16, 5800 AA Venray, The Netherlands

VOORWOORD

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CONTENTS

1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Selection of breeding pigs for fattening and carcass traits generally takes place at central test stations. In relation to other traits, daily feed intake is an important trait for selection on performance. Till now, individual feed intake recordings only have been possible by testing pigs in individual pens. Ketelaars (1979) and Merks (1989) showed, that rather low genetic correlations exist between central test and commercial fattening results, due to genotype x environment (GxE) interactions. However, Crump et al. (1990) and Van Diepen and Kennedy (1989) found no evidence for GxE interactions. As commercial fattening pigs are housed in groups, genotype x housing system (GxH) interactions can contribute to possible GxE interactions.

The main difference between individual and group housing is probably the occurrence of social interactions between animals, like competition for the feed and stimulation of eating by seeing other pigs eating (social facilitation). Social ranking may influence daily feed intake and growth rate (McBride et al., 1964). Wittmann (1981 and 1983) showed that housing system (individual *v.* group housing) significantly influenced daily eating time, rate of feed intake and frequency of eating. Individually housed pigs had a higher daily feed intake and higher growth rate than group housed pigs. These results indicate, that housing system influences feed intake pattern, i.e. the distribution of feed intake over meals and over the day. In turn, feed intake pattern may be related with performance.

Feed intake pattern and performance can be related through many pathways. First of all there may be a relation through digestibility. A second group of relations occurs with utilisation of energy and nutrients after they have been absorbed. The availability of amino acids may be altered by pattern of feed intake (Batterham and Bayley, 1989;

Den Hartog et al., 1979). In addition, feed intake activity may vary and thus also alter heat production and overall efficiency (Braastad and Katle, 1989; Luiting, 1991).

The main aim of this thesis is to investigate relationships between feed intake pattern and performance. Knowledge of relationships between feed intake pattern and production traits can be important for pig breeding. These relationships may be associated with part of the occurrence of GxH interactions. Furthermore, feed intake pattern may also be used for selection of those pigs with the best feed utilisation. Subjects to be addressed are:

1) Effects of housing system on feed intake pattern and production traits.
2) Effect of feed intake pattern on production traits.
3) Genetic aspects of feed intake pattern.

In Chapter 1 the IVOG®-station is described. This feeding station enables testing of pigs in group pens under competition, with individual feed intake recording. At each visit of a pig to the IVOG-station the animal identification number, beginning and end time and beginning and end weight of the feed are recorded. From these data not only individual daily feed intake, but also the feed intake pattern can be derived.

Data were collected of Dutch Landrace (DL) pigs, housed in individual and in group pens, during three batches. Individual feed intake and feed intake pattern were recorded by using IVOG-stations. Performance traits, like growth rate during test, ultrasonic backfat thickness, feed conversion and lean percentage were also measured. Differences in feed intake pattern and production traits between individual and group housing are analysed in Chapter 2. In Chapter 3 individual digestibility coefficients of pigs, housed in both housing systems, are determined to investigate the effect of housing system on digestibility. The relationships between feed intake pattern and digestibility are analysed and housing system effects on these relationships are investigated.

After three batches with individual and group pens, data were collected in group housing during two batches, with Great Yorkshire (GY) as well as DL pigs. These data, together with the group housing data of the first three batches, are used to estimate genetic effects and relationships between feed intake pattern and performance traits in group housing.

In Chapter 4 individual residual daily feed intake (RFID) is estimated, as a measure for efficiency of production (Foster et al., 1983; Luiting and Urff, 1987). RFID is defined as the difference between the observed feed intake of an animal and its predicted feed intake, based on metabolic body weight and production traits. The effects of feed intake activity and feed distribution (over meals) on efficiency of production are analysed by estimating relationships between feed intake pattern, RFID, growth rate and body composition.

Genetic aspects, like breed effect, sex effect and heritabilities for feed intake traits, are investigated in Chapter 5. Differences in feed intake pattern between DL and GY pigs are determined, with possible implications for performance.

In the General Discussion differences in feed intake pattern between individual and group housing and differences in trait relationships between individual and group housing are evaluated. These differences are also examined as possible explanations for GxH interactions. It is discussed by what mechanisms feed intake pattern can be related to production traits. Finally, the value of individual feed intake recording for selection of breeding pigs is evaluated.

REFERENCES

Batterham, E.S. and Bayley, H.S., 1989. Effect of frequency of feeding of diets containing free or protein bound lysine on the oxidation of [^{14}C]lysine or [^{14}C]phenylalanine by growing pigs. Br. J. Nutr., 62:647-655.

Braastad, B.O. and Katle, J., 1989. Behavioral differences between laying hen populations selected for high and low efficiency of food utilization. Br. Poultry Sci., 30:533-544.

Crump, R.E., Thompson, R. and Mercer, J.T., 1990. The genetic relationship between sexes for pig performance traits as recorded in a commercial Landrace nucleus herd. 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, Great Britain, XV:454-457.

Den Hartog, L.A., Verstegen, M.W.A. and Huisman, J., 1989. Amino acid digestibility in pigs as affected by diet composition. In: Friedman, M. (Ed.), Absorption and utilization of amino acids, Vol. III., CRC Press, Florida, pp. 201-216.

Foster, W.H., Kilpatrick, D.J. and Heaney, I.H., 1983. Genetic variation in the efficiency of energy utilization by the fattening pig. Anim. Prod., 37:387-393.

Ketelaars, E.H., 1979. De vererving van onder praktijkomstandigheden geregistreerde kenmerken bij varkens. Verslag Landbk. Onderz., 883. Pudoc, Wageningen.

Luiting, 1991. The value of feed consumption data for breeding in laying hens. PhD Thesis, Wageningen Agricultural University, The Netherlands.

Luiting, P. and Urff, E.M., 1987. Residual feed intake: a new source of genetic variation for feed efficiency. 38th Annual Meeting of the European Association for Animal Production, Lisbon, Portugal, GNC4.8: 6 pp.

McBride, G., James, J.W. and Hodgens, N., 1964. Social behaviour of domestic animals. IV. Growing pigs. Anim. Prod., 6:129-139.

Merks, J.W.M., 1989. Genotype x environment interactions in pig breeding programmes. VI. Genetic relations between performances in central test, on-farm test and commercial fattening. Livest. Prod. Sci., 22:325-339.

Van Diepen, T.A. and Kennedy, B.W., 1989. Genetic correlations between test station and on-farm performance for growth rate and backfat in pigs. J. Anim. Sci., 67:1425-1431.

Wittmann, M., 1981. Verbesserung des technischen und biologischen gleichgewichtes der industriemässigen schweinefleischproduktion mit hilfe der verhaltensforschungsergebnisse. Int. Symposium on Applied Animal Ethology, Gödöllö, Hungary. pp. 51-63.

Wittmann, M., 1983. Gruppeneffect auf das fressverhalten. Int. Sci. Symposium on Applied Animal Behaviour, Nitra, Czechoslovakia.

Chapter 1

A NOTE ON THE IVOG®-STATION: A FEEDING STATION TO RECORD THE INDIVIDUAL FEED INTAKE OF GROUP HOUSED GROWING PIGS

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ABSTRACT

A feeding station is described that is used for individual feed intake recordings of group housed growing pigs. The IVOG®-station can be used for performance testing in group housing or for investigating effects of, for example housing system, feed composition, breed or sex on feed intake pattern and production traits.

INTRODUCTION

In pig breeding programmes selection at nucleus level for growth rate, feed intake and slaughter quality usually takes place through performance testing at central test stations. Pigs are housed individually to measure the individual feed intake of each pig. This is in contradiction to group housing in commercial fattening. Therefore, a disadvantage of the normal used test system is that genotype x housing system (individual *v.* group housing) interactions may exist and contribute to genotype x environment interactions. A result of genotype x housing system interactions may be that moderate genetic relationships occur between performances at nucleus level and performances at commercial fattening level (Merks, 1989), which will reduce the efficiency of the breeding programme. To avoid genotype x housing system interactions, testing should take place in group housing. An advantage of group housing is also the lower level of housing system costs per test place.

At our institute a feeding station has been developed to measure individual ad libitum feed intake of growing pigs in group housing. This station, referred to as IVOG®-station (Individual VOluntary feed intake recording in Group housing) was developed in cooperation with TFDL (Technical and Physical Service in Agriculture), Wageningen, The Netherlands. With the IVOG-station daily feed intake patterns may be deduced from individual feed intake data. Experiments are performed to analyse the effect of housing system on feed intake patterns (De Haer and Merks, 1992).

MATERIAL AND METHODS

Equipment

The IVOG-station consists of a free hanging feed hopper with a reservoir of a maximum of 30 kg of dry feed, a load cell to weigh the hopper, a photocell to detect pigs entering the station and an antenna to read the identification codes of the pigs. The load cell weighs with an accuracy of ± 10 grams, within a range of 0 to 50 kg. If the photocell is not interrupted the feed hopper is weighed continually. Each pig carries an ear transponder, that is activated by the antenna within a range of 60 cm.

TABLE 1. Example of feed intake data per visit, recorded with an IVOG-station.

1	2	3	4	5	6	7	8
18	259	317	21640	841	21306	1	4
18	261	854	21303	1031	21185	1	4
18	261	1348	21187	1402	21155	1	4
18	255	1429	21161	1656	21006	1	4
18	255	1706	21006	1806	20933	1	4
18	258	1809	20933	1947	20803	1	4
18	255	2020	20803	2305	20597	1	4
18	255	2318	20597	2519	20434	1	4
18	261	21054	20428	21538	20010	1	4
18	257	61705	19993	61929	19904	1	4
18	260	61939	19907	62203	19769	1	4
18	262	63352	19763	63710	19589	1	4
18	258	70720	19585	71547	19065	1	4
18	257	74403	19091	75215	18568	1	4
18	261	92429	18568	92809	18338	1	4
18	260	92815	18343	92945	18240	1	4
18	260	93125	18240	93312	18107	1	4
18	261	94059	18105	94102	18081	1	4
18	261	94322	18105	94343	18069	1	4
18	261	95434	18080	100452	17528	1	4
18	257	100546	17527	100930	17383	1	4
18	256	101144	17377	101527	17208	1	4
18	257	101548	17208	102112	16969	1	4

Column 1: pen number
2: animal identification number
3: time at beginning of visit (h-min-sec)
4: weight of feed at beginning of visit (g)
5: time at end of visit (h-min-sec)
6: weight of feed at end of visit (g)
7: day
8: month

A small fence in front of the feed hopper extends 25 cm into the pen, to make a clear distinction in time between two successive visits. The entrance to the feeder is open. The fence is small enough to make competition among pigs possible. The entrance width can be adjusted between 20 to 35 cm, depending on the size of the pigs, to prevent two pigs entering the station at the same time. When a pig enters the IVOG-station the photocell is interrupted and time, weight of the feed and pig identification number are collected. At the end of the visit, when the light beam is not interrupted, time and weight of the feed are collected again. After each visit the following data are recorded: pen number, animal identification number, time and weight of the feed at the beginning and time and weight of the feed at the end of the visit and date of visit. Thus, for each visit, duration and feed intake are known. An example of the output is shown in Table 1.

Entrance to the feed hopper is blocked by a partition when the hopper is filled up, because at that moment no feed intake recordings can take place. Water is supplied outside the feeding station. Supply inside the IVOG-station would disturb the weight measurements.

Test data

At the Bantham experimental farm 20 pens were equipped with IVOG-stations. During five batches feed intake data were recorded of group-housed and individually housed pigs. A group consisted of eight pigs. The pigs were tested from a live weight of 25 to 35 kg until an average weight per pen of 100 kg.

RESULTS AND DISCUSSION

Accuracy

Every time the hopper was filled, the amount of feed added was recorded using a separate scale. To estimate the accuracy of the IVOG-stations, the recorded total feed intake per pen and the total amount of feed put in the feed hopper were compared.

In 87 of 90 cases (5 batches with 20 feed hoppers, but during two batches not all pens were used) IVOG-stations recorded less total feed intake during test than total feed intake based on data of filling the feed hoppers. The average value was proportionately 0.96 recorded of total feed supplied. This means that total feed intake was on average underestimated by 0.04.

Underestimation of real feed intake could be due to wasting feed when the hoppers were filled. As a consequence, registrations of feed supplies were higher than the feed truly put in the hoppers.

Inaccuracy of weighing feed was mainly due to two problems. The main problem that caused inaccurate weighings was the accumulation of dirt under the feed hoppers. This problem was due to a small chink under the edge of the through that could not be closed, because the hopper had to hang freely. Regularly some feed hoppers had to be detached from the weighing part to remove the dirt. Inaccurate weighings were corrected for on basis of eating time, but this was an approximation of real feed intake. The design of new IVOG-stations is improved to prevent the influence of dirt on weighings as much as possible. An other problem common to all batches was the loss of ear tags, mostly because other pigs chewed on it and the plastic tag holder broke down. This influenced accuracies of feed intake recordings per pig. The proportional losses per batch varied from 0.12 to 0.20. When a pig had lost its ear tag, visits were still recorded, but without an animal identification number. Afterwards, these recordings could be traced back to the right animal. But when more than one pig in a pen had lost the ear tag, the amount of feed eaten by unidentified pigs was divided equally among the pigs concerned. This caused inaccurate feed intake recordings, because equal division of feed was only an approximation of the real feed intake of each pig. When injectable identification transponders become available, these implants will be used for more accurate identification.

Comparison with other equipment

The main difference between the IVOG-station and other feeding stations for growing pigs (e.g. Bartussek and Hausleitner, 1987; Slader and Gregory, 1988) is the entrance to the feeder. At the IVOG-station the entrance is open and when a pig stands eating, the back and sides are unprotected. Pigs can be chased away from the feeder by competition with other pigs. In other feeding stations a pig can eat undisturbed, protected by a crate-like entrance. It is assumed that competition is a main factor in group housing and therefore a necessary element to include for testing of breeding pigs in order to prevent genotype x housing system interactions. Furthermore, an advantage of the IVOG-station is its relatively simple design; a disadvantage is that no restricted feeding can take place.

Final remarks

Apart from using IVOG-stations for testing of breeding pigs, there are many other possibilities for use in research centres, like determining the effect of different kinds of feed on feed intake pattern. Appetite of different pig breeds or different sexes can be compared. Under varying housing systems the effects on feed intake traits and related effects on production traits can be determined. For a description of feed intake pattern within individual and group housing, see De Haer and Merks (1992).

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REFERENCES

Bartussek, H. and Hausleitner, A., 1987. Electronische abruffütterung und einzeltierherkennung bei mastschweinen in gruppenhaltung. Aktuelle Arbeite zur artgemässen Tierhaltung. KTBL-Schrift 323, p.198-213.

De Haer, L.C.M. and Merks, J.W.M., 1992. Patterns of daily feed intake in growing pigs. Anim. Prod., 54 (in press).

Merks, J.W.M., 1989. Genotype x environment interactions in pig breeding programmes. VI. Genetic relations between performances in central test, on-farm test and commercial fattening. Livest. Prod. Sci., 22:325-339.

Slader, R.W. and Gregory, A.M.S., 1988. An automatic feeding and weighing system for ad libitum fed pigs. Comp. and Elec. Agric., 3:157-170.

Chapter 2

PATTERNS OF DAILY FEED INTAKE IN GROWING PIGS

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PATTERNS OF DAILY FEED INTAKE IN GROWING PIGS

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ABSTRACT

Feed intake patterns of growing pigs given feed ad libitum in individual and group housing were derived from feed intake recordings with IVOG®-stations. The IVOG-station is a feeding station that records animal identification number, time, duration and amount of feed intake during each visit of a pig to the feed hopper. The objective was to describe and evaluate feed intake patterns of growing pigs in individual and in group housing. Data were collected in three testing batches of 90 Dutch Landrace pigs each, housed in 10 individual pens and in 10 group pens of eight pigs per batch.

Based on survival analysis theory, intervals between visits shorter than five minutes (which was used as meal criterion) were regarded as within-meal intervals and these visits were grouped into meals. In group housing, feed intake per day and rate of feed intake had no significantly non-normal distribution. In individual housing feed intake per day, rate of feed intake and number of meals per day had no significantly non-normal distribution. All traits were normally distributed after discarding extreme values, except eating time and feed intake per visit and per meal. In group housing these traits were not significantly non-normally distributed after logarithmic transformation.

Pigs housed in groups ate faster, had a higher feed intake per meal but less meals per day, less eating time per day and a slightly lower daily feed intake than pigs

penned individually. During the day two peaks of feeding activity occurred, especially in group housing: one in the morning and one in the beginning of the afternoon.

A distinction was made between meals with a major contribution to daily feed intake and meals of minor importance. In group housing 69% of the daily number of meals accounted for proportionately 0.87 of daily feed intake and 0.83 of daily feed intake time. In individual housing 39% of the meals accounted for 0.90 of the daily feed intake and 0.79 of the daily eating time.

Repeatabilities of day to day recordings of feed intake traits, were higher within individual than in group housing. Frequency and rate of feed intake were relatively highly repeatable traits.

INTRODUCTION

In pig breeding programmes, genotype x environment interactions may be present across levels of the breeding programme (Merks, 1989). The presence of these interactions indicates that differences in environment between central test and commercial fattening may result in selection of boars which are not the best for use in commercial fattening. Being part of the environment, housing system may contribute to genotype x environment interactions, because in central test stations individual housing is applied, while fattening pigs are housed in groups. To study the influence of housing system on production traits and feed intake characteristics, the IVOG®-station was developed. The IVOG-station combines housing of pigs in groups with recording of individual feed intake while competition for the feed is maintained (De Haer et al., 1992). Without having to press a bar, a pig can eat ad libitum from a continuously weighed feed hopper.

Fat and protein deposition may be influenced by feed intake characteristics like frequency of feed intake and meal size (Cohn et al., 1962; Foster et al., 1983). To use these characteristics in pig breeding, a sufficient repeatability between daily values is important. A high repeatability indicates that measurements during a part of the testing period are good predictors of values measured during the whole fattening period.

The objective of this study is to describe and evaluate objectively recorded feed intake patterns of growing pigs, housed individually or in groups. In a subsequent paper these traits will be related to production traits, especially for group housed pigs.

MATERIAL AND METHODS

Experimental design

At the Bantham experimental farm three batches of purebred Dutch Landrace boars and gilts were tested from August 1988 till October 1989. Each batch comprised ten individual and ten group pens. A group consisted of eight pigs, generally not litter-mates, penned together according to weight. In each group one pig had a litter-mate in individual housing. To minimise the variation in final weights within a pen, each pen comprised either boars or gilts.

To identify individual animals, each pig had an ear responder. Feed was supplied ad libitum. Each pen was equipped with an IVOG-station (De Haer et al., 1992). The IVOG-station consists of a single space feed hopper which is weighed continuously, and an antenna to read the ear responder. To enable competition for food, the entrance to the hopper is always open. Each visit of a pig to the feed hopper, time and weight of the feed at the beginning and at the end of the visit are recorded, together with the identification number of the animal.

During the test only some daylight entered the unit. The feed at the beginning of test contained a Net Energy of 9.4 MJ per kg and 183 g/kg of crude protein, of which 50 kg per pig was supplied. The feed used for older pigs was a commercial feed for growing pigs, with a Net Energy of 9.1 MJ per kg and 168 g/kg of crude protein. The floor surface per pig was 0.76 m^2 in group housing and 3.27 m^2 in individual housing. The floor was half slatted.

The test period started at a live weight between 25 and 35 kg and finished at an average pig weight within a pen of at least 100 kg. Slaughtering of pigs was once a week. At an age of 170 ± 10 days backfat thickness was measured ultrasonically and the pigs were weighed. When the test was finished, live weight was recorded and lean meat percentage (ham + shoulder + loin + lean offal, bone included) was determined according to the IVO standard dissection method (Bergström and Kroeske, 1968).

Meal criterion

The feeding rhythm is characterised by an alternation of 'meal' and 'interval' states (Metz, 1975). A meal consists of alternations of 'feeding bouts' (visits) with short within-meal intervals. Meals are separated by between-meal intervals that are longer and occur less frequently than within-meal intervals (Wiepkema, 1968). To decide if an interval is a within-meal interval or a between-meal interval a meal criterion (m.c.) was defined. The m.c. is the maximum length of the within-meal interval (Duncan et al., 1970; Metz, 1975; Salden en Sas, 1976). The m.c. enables grouping of individual visits, separated by intervals shorter than the m.c., to one meal.

A survivorship curve was used to determine the m.c., in which the cumulative frequencies of interval lengths between visits were plotted on a logarithmic scale. Assuming that the moment of beginning of a visit is independent of the moment of finishing the previous visit, the cumulative frequencies of interval lengths between visits will be exponentially distributed, resulting in a straight line when plotted on a logarithmic scale (Metz, 1975). Cumulative frequencies of intervals between dependent visits (within a meal) will show a concave curve when plotted on a logarithmic scale. The m.c. was estimated for each pig by approximating the log survivorship curve of intervals between visits partly with a curved and partly with a linear function (Genstat 5 Committee, 1987). There are relatively many within-meal intervals, which are described by the left part of the curve. The straight line describes between-meal intervals. The m.c. is the breakpoint in the curve, where the concave curve (left part) changes into a straight line (right part). The following polynomials were used to estimate the breakpoint (γ) iteratively:

$$x \leq \gamma : Y = \mu + a_1(x-\gamma) + a_2(x-\gamma)^2 + a_3(x-\gamma)^3 + e \qquad \text{polynomial of order 3}$$
$$x > \gamma : Y = \mu + b_1(x-\gamma) + e \qquad \text{polynomial of order 1}$$

where: Y = log(1 - cum.freq.(x)); x = interval length (min); γ = breakpoint (m.c.), in which $x = \gamma$ and $E(Y) = \mu$

For the left part the order 3 was chosen, because in preliminary analyses the regression coefficient a_3 was often highly significant ($P<0.01$). The coefficient b_1 was also highly significant ($P<0.01$).

The variation in m.c. between animals within housing systems was analysed. For each pig, data of the whole fattening period were used to estimate the m.c. in order to have enough data to make an accurate estimation. Three sets of data were analysed: (1) all data of group housed pigs (229 pigs), (2) data of group housed pigs of visits that were followed by visits of the same animal (229 pigs) and (3) data of individually housed pigs (30 pigs). Data set 2 represents visits of pigs that were not chased away but continued their meal after a short interruption. After determining the m.c. in each data set, the influence of varying m.c. on relationships between feed intake characteristics was analysed.

Feed intake pattern

When an m.c. was chosen, visits could be grouped to meals. Within a day, the amount of feed intake per meal was varying. To distinguish between pigs with a few large meals per day (meal eaters) and pigs with many small meals (nibblers) the

Linda-index (De Jong, 1985) was used. This index determines the number of meals that have a major contribution to the daily feed intake and the number of meals that are of minor importance. This index is used for instance in statistical studies to determine the number of leading companies with largest market share ('oligopolists') in an industry. It also determines the measure of inequality in market share between the companies. With this index the first important discontinuity between the values of meal sizes, ordered in descending order, is determined. After reaching a minimum value for k meals the index for $k + 1$ meals has a larger value. The number of meals of major contribution is k. When the index is always decreasing, k is set equal to the total number of meals for that day. Within each day the share of k largest meals in relation to the total daily feed intake was calculated.

$$Q_i = \frac{A_i \,/\, i}{(A_k - A_i) \,/\, (k-i)}$$

$$L_k = \frac{\sum_{i=1}^{k-1} Q_i}{k \times (k-1)}$$

where: n = number of meals on a day; $k = 2,...,n$; k largest meals within n; $i = 1,...k\text{-}1$; i varies within each k; A_i = total share of i meals (kg) within k largest meals; A_k = total share of k largest meals (kg) within n meals on a day; Q_i = average share of i meals in relation to the average share of the $k\text{-}i$ remaining large meals; L_k = Linda-index for k largest meals = $1/k$ multiplied by the average of the Q_i's

The following feed intake traits were analysed within and among housing systems:

TV = average eating time per visit (min)
TM = average eating time per meal (min)
TD = average eating time per day (min)
TDLX = daily eating time in NLX large meals (min)
NVD = number of visits per day
NMD = number of meals per day
NLX = number of meals of major importance (according to Linda-index)
FIV = average feed intake per visit (g)
FIM = average feed intake per meal (g)
RFI = average rate of feed intake (g/min) (=FID/TD)
FID = average feed intake per day (g)
FILX = daily feed intake in NLX large meals (g)

Statistical analysis

To test feed intake traits for normality, skewness and kurtosis were calculated for average values during the test period for each animal. In addition Shapiro and Wilk's W test for normality was used (Shapiro and Wilk, 1965). This test is especially sensitive to asymmetry, long tailedness and to some degree to short tailedness. It was developed for small samples and extended by Royston (1982a) as a test for large samples. Algorithms described by Beasley and Springer (1977), Hill (1973) and Royston (1982b and 1982c) were used to apply the W test. Small values of W indicate non-normality, the significance is given by percentage points of the distribution of W. Extreme values were discarded when the value was outside the interval of ± 2 standard deviations around the mean.

To obtain more information about the variation in traits from day to day in the test period, repeatabilities of daily values of feed intake characteristics within animals and periods of a week to a month were estimated. It was assumed that variances of the different measurements were equal and that different measurements reflect the same character. Therefore, corrections for weeks were performed when data were evaluated over longer periods and age of the animals influenced the traits. Within housing system variance components between animals and within animals (σ^2_{wa} and σ^2_{ba}) were estimated (Harvey, 1977) according to the following two models:

within two-week periods in the fattening period:

$$Y_{ij} = \mu + a_i + e_{ij} \tag{model 1}$$

within each month in the fattening period and within the whole fattening period:

$$Y_{ijk} = \mu + a_i + w_j + e_{ijk} \tag{model 2}$$

where: Y_{ijk} = value of feed intake characteristic for each animal at each day; a_i = effect of the i-th animal (random); w_j = effect of the j-th week (fixed); e_{ijk} = residual error

The repeatability r was estimated as:

$$r = \frac{\sigma^2_{ba}}{\sigma^2_{ba} + \sigma^2_{wa}}$$

where: σ^2_{ba} = variance between animals (= genetic variance + general environmental variance); σ^2_{wa} = variance within animals (= special or temporarily variance)

To estimate the repeatability without disturbances by starting and finishing, the test data from the first three weeks and last four weeks were not included. During the last four weeks the number of animals that were present was not constant, because every week a number of pigs was slaughtered.

RESULTS

As an example, in Figure 1 feed intake per visit versus time during the day is plotted for two littermates during a randomly chosen day. One pig was penned individually and one was penned in a group. This figure shows that several visits to the hopper occur with very small time intervals in between, especially for the individually penned pig. By choosing a suitable m.c., such visits can be grouped to one meal.

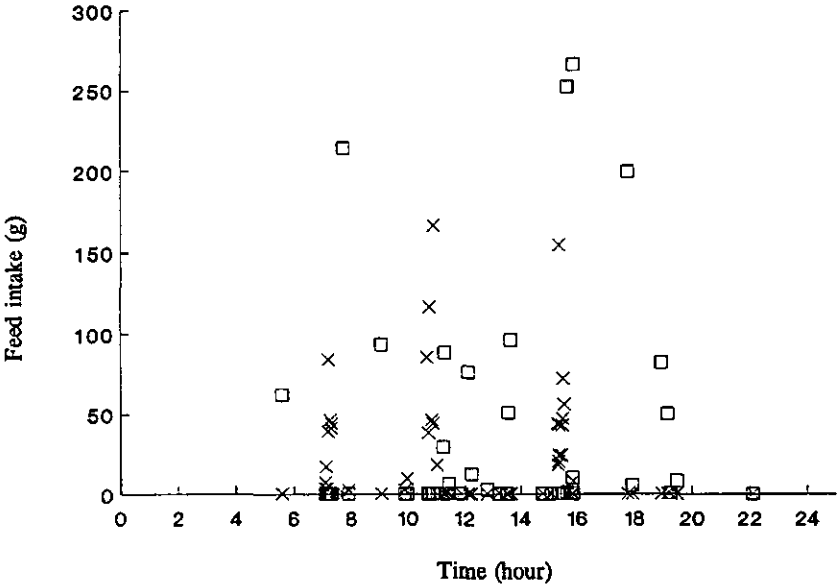

FIGURE 1. Distribution of feed intake of two littermates, one in group housing (□) and one in individual housing (×), on a randomly chosen day.

The m.c. was determined within pigs. Using the model with a polynomial of order 3 as left part and a straight line as right part showed small differences between residual variances for different m.c. within a pig. In Figure 2 the distributions of m.c. are shown. Data sets 1 and 2 consisted both of visits of group housed pigs, but in data set 2 only the visits that were followed by a visit of the same animal were included. Visits of pigs that were chased away were excluded. The differences in m.c. between data set 1 and data set 2 were small, but estimates of m.c. with data set 2 had lower accuracies (larger residual variances). In group housing the average m.c. was five minutes, in individual housing (data set 3) the average m.c. was six minutes with almost similar residual variances.

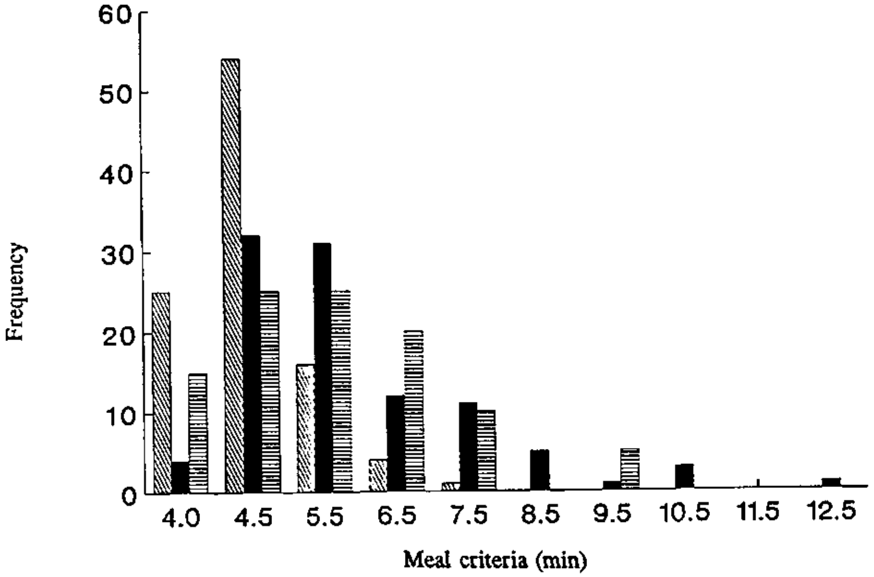

FIGURE 2. Distribution of meal criteria, determined by using all data of group housed pigs (\\\), group housing data consisting of visits that were followed by a visit of the same animal (■) and data of individually housed pigs (≡).

For both housing systems a m.c. of five minutes was used to characterise clusters of visits to the feed hopper as meals. The reason to choose one m.c. was to create the possibility of comparing time and feed intake per meal and number of meals per day across housing systems.

Averages and standard deviations of feed intake characteristics are given in Table 1. Visits and meals at which no feed was ingested were not included. Total daily eating time was larger in individual housing, mainly because there were more meals per day. Feed intake per meal was larger in group housing than in individual housing. Although rate of feed intake was lower in individual housing, the pigs had a higher feed intake per day because of a longer eating time per day. According to the Linda-index, in group housing 69% of the number of meals per day accounted for proportionately 0.87 of the total daily feed intake and 0.83 of daily eating time, therefore 31% of the meals were small meals of short duration. In individual housing 39% of the number of meals per day accounted for proportionately 0.90 of the daily feed intake and 0.79 of the daily eating time, consequently the relative amount of small meals was much larger in individual housing.

TABLE 1. Feed intake characteristics within individual and group housing. The meal criterion is five minutes.

	Group housing		Individual housing	
	Average	s.d.	Average	s.d.
Time per visit (TV) (min)	4.7	(1.5)	1.5	(0.8)
Time per meal (TM) (min)	6.9	(1.8)	4.2	(1.6)
Time per day (TD) (min)	63.5	(13)	84.1	(15)
Time per day in large meals (TDLX) (min)	52.6	(12)	66.1	(13)
No. of visits per day (NVD)	14.4	(5.0)	58.6	(19)
No. of meals per day (NMD)	9.2	(2.4)	20.1	(4.9)
No. of large meals per day according to Linda-index (NLX)	6.3	(1.7)	7.8	(3.2)
Feed intake per visit (FIV) (g)	158.8	(50)	37.8	(17)
Feed intake per meal (FIM) (g)	225.0	(59)	110.0	(38)
Rate of feed intake (RFI) (g/min)	32.0	(5.0)	27.2	(5.0)
Feed intake per day (FID) (g)	2043	(291)	2203	(200)
Feed intake per day in large meals (FILX) (g)	1774	(352)	1987	(190)

TABLE 2. Correlations between eating time per day (TD), daily feed intake (FID), number of visits or meals per day (NVD or NMD) and feed intake per visit or per meal (FIV or FIM) using meal criteria of four (FIM1, NMD1) and eight (FIM2, NMD2) minutes.

	Group housing	Individual housing
TD - FIV	-0.16	0.11
TD - FIM1	-0.05	-0.20
TD - FIM2	0.01	-0.23
TD - NVD	0.50	-0.13
TD - NMD1	0.41	-0.04
TD - NMD2	0.38	0.01
FID - FIV	0.03	0.18
FID - FIM1	0.20	0.48
FID - FIM2	0.29	0.64
FID - NVD	0.48	0.20
FID - NMD1	0.39	-0.05
FID - NMD2	0.33	-0.20
NVD - NMD1	0.89	0.69
NVD - NMD2	0.87	0.52
FIV - FIM1	0.92	0.82
FIV - FIM2	0.87	0.75

To investigate the influence of different m.c. on feed intake characteristics, the correlations between characteristics were calculated with two m.c. values (Table 2) of four and eight minutes. The correlations indicate that grouping visits into meals had more influence on correlations in individual housing than in group housing. In both housing systems, choosing a meal criterion of four or eight minutes, had no large influence on estimated correlations, except for the correlation between FID and FIM in individual housing.

TABLE 3. Shapiro-Wilk test for normality, skewness and kurtosis of untransformed feed intake traits. Skewness and kurtosis of traits transformed by the natural logarithm and of traits with discarded extreme values.

	Untransformed			Log(e) Transformation		Discarded Extremes	
	W-test	skew.	kurt.	skew.	kurt.	skew.	kurt.
Group housing							
TV	0.912**	1.282**	2.396**	0.330	0.204	0.549**	-0.033
TM	0.938**	0.922**	0.980**	0.211	-0.222	0.351*	-0.377
TD	0.976*	0.638**	1.045**	-0.177	1.096**	0.220	-0.369
TDLX	0.965**	0.755**	1.081**	-0.004	0.346	0.194	-0.645**
NVD	0.958**	0.763**	0.880*	-0.117	-0.003	0.333*	-0.371
NMD	0.960**	0.434**	-0.070	-0.179	-0.228	0.256	-0.680**
NLX	0.925**	0.669**	0.234	-0.011	-0.245	0.353*	-0.587*
FIV	0.919**	1.244**	2.451**	0.087	0.455	0.404*	-0.215
FIM	0.956**	0.859**	1.315**	-0.161	0.893*	0.325	-0.462
RFI	0.983	-0.209	1.108**	-1.390**	6.452**	0.119	-0.446
FID	0.970*	0.112	1.860**	-0.993**	4.523**	0.214	-0.157
FILX	0.983	0.048	0.238	-0.621**	0.621*	-0.156	-0.447
Individual housing							
TV	0.772**	1.959**	3.770**	1.056*	0.798	1.495**	2.398**
TM	0.816**	1.433**	1.297*	0.918*	0.288	1.155**	1.552*
TD	0.835**	2.009**	6.022**	1.208**	3.037**	-0.020	-0.263
TDLX	0.863**	1.854**	6.062**	0.857*	2.733**	0.334	0.736
NVD	0.962	-0.141	-0.053	-1.227**	2.315**	0.501	-0.883
NMD	0.975	-0.307	0.513	-1.074*	1.467*	-0.595	0.193
NLX	0.874**	1.572**	4.105**	0.340	0.416	0.405	-0.480
FIV	0.651**	2.853**	8.768**	1.499**	3.198**	0.208	-1.036*
FIM	0.768**	1.967**	3.799**	1.289**	1.422*	1.265**	1.143*
RFI	0.957	-0.826	1.834*	-1.841**	5.985**	0.091	-0.716
FID	0.978	-0.375	1.394*	-0.909*	2.528**	0.005	-0.263
FILX	0.985	-0.173	1.122*	-0.667*	1.738*	-0.069	-0.192

probabilities:

* = $P < 0.05$

** = $P < 0.01$

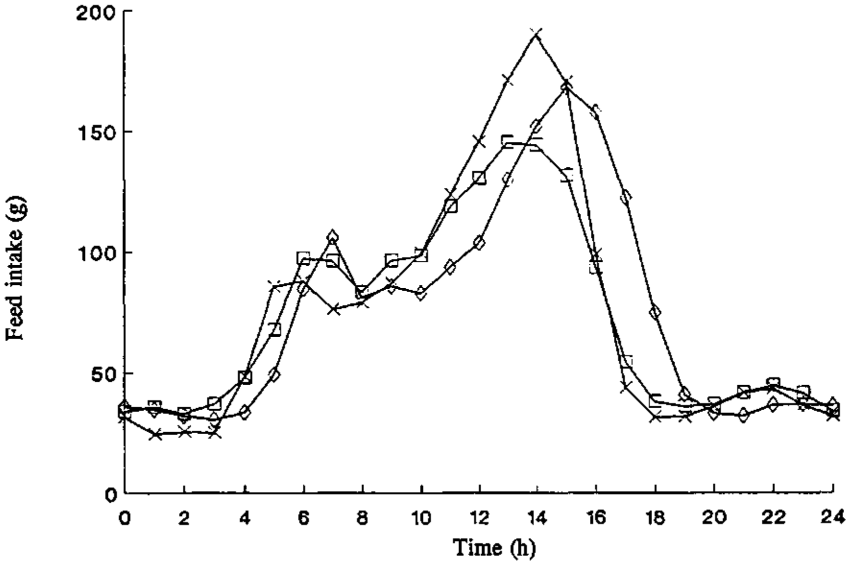

FIGURE 3. Average feed intake (g) per h for group housed pigs in batch 1 (□), batch 2 (×) and batch 3 (◇).

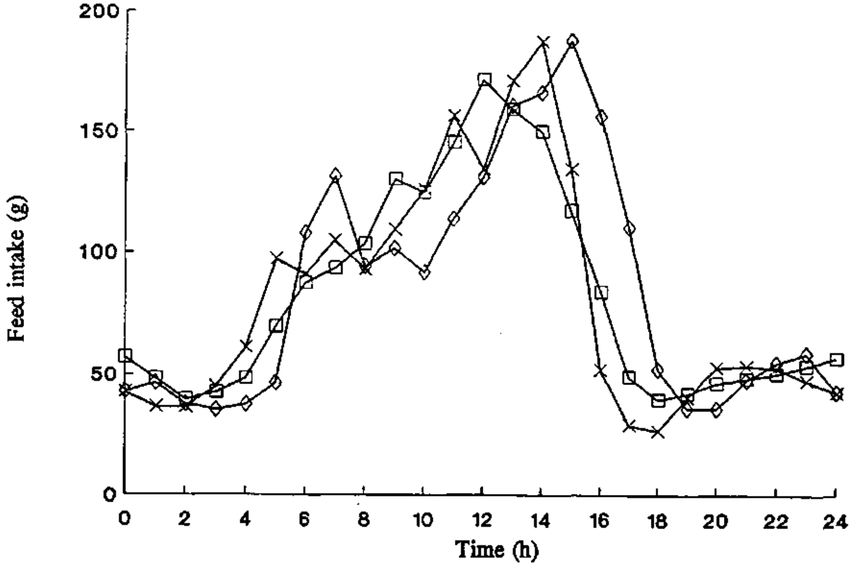

FIGURE 4. Average feed intake (g) per h for individually housed pigs in batch 1 (□), batch 2 (×) and batch 3 (◇).

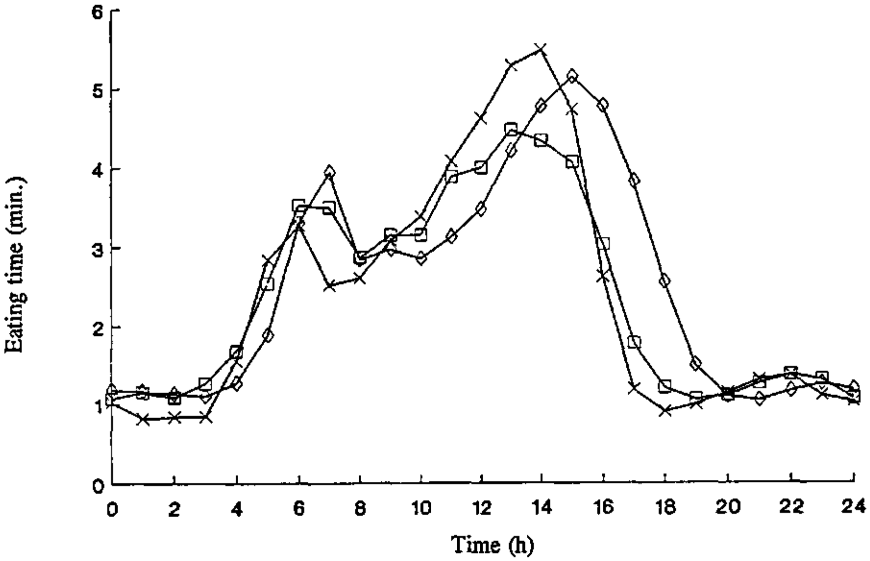

FIGURE 5. Average eating time (min) per h for group housed pigs in batch 1 (□), batch 2 (×) and batch 3 (◇).

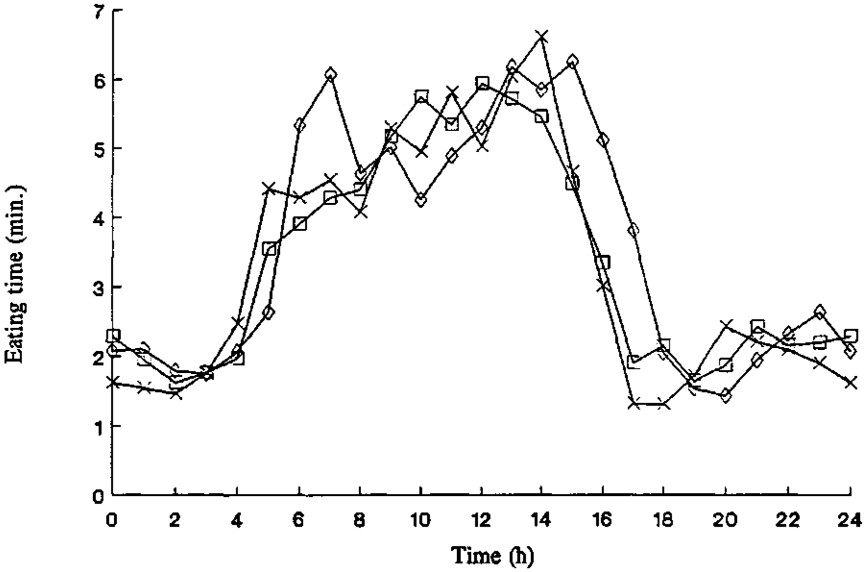

FIGURE 6. Average eating time (min) per h for individually housed pigs in batch 1 (□), batch 2 (×) and batch 3 (◇).

Skewness, kurtosis and results of the W test for normality are presented in Table 3. Expected value under normality for the W-test is one. Skewness and kurtosis under normality are expected to be zero. The coefficients for skewness and kurtosis and the W-test gave comparable results. In group housing rate of feed intake and feed intake per day in the largest meals had no significantly non-normal distribution. Feed intake per day had no significantly skewed distribution. Time per visit and per meal and feed intake per visit and per meal had skewed distributions with high kurtosis. After logarithmic transformation (natural logarithm) these traits became not significantly non-normally distributed. After discarding extreme values (14) skewness and kurtosis were reduced considerably, but skewness was highly significant for time per visit (TV). In individual housing rate of feed intake, feed intake per day and feed intake per day in the largest meals together with number of visits per day and number of meals per day had no significantly non-normal distribution. The traits feed intake per meal and per visit, time per meal and per visit and time per day had a very skewed distribution with a high kurtosis. They did not become normally distributed after logarithmic transformation. Number of largest meals per day and time per day in the largest meals were not significantly non-normally distributed after logarithmic transformation. After discarding extreme values (3) all traits had no significantly non-normal distribution, except FIM, TM and TV which had very skewed distributions.

In Figures 3, 4, 5 and 6 the distribution of feed intake and eating time during the day are given, based on data of three batches. In both housing systems, the largest feed intake occurred from 11.00h to 16.00h. In batch 3 the feed intake pattern was shifted one hour compared to patterns in batch 1 and 2. In group housing between 5.00h and 8.00h and between 11.00h and 16.00h most time was spent eating. In individual housing the time spent eating per hour was more equally distributed from 5.00h to 15.00h, with a peak around 14.00h. In batch 3 two peaks in eating time occurred, both for group housed pigs and individually housed pigs.

TABLE 4. Average repeatabilities for daily feed intake traits in individual and group housing. Estimations are made within the total fattening period, within months and within two-week periods.

	Group housing			Individual housing		
	Total	Month	2-Week	Total	Month	2-Week
TV	0.16	0.25	0.39	0.36	0.35	0.70
TM	0.21	0.26	0.38	0.31	0.41	0.60
TD	0.22	0.26	0.40	0.04	0.10	0.63
NVD	0.12	0.24	0.50	0.45	0.45	0.60
NMD	0.24	0.29	0.42	0.58	0.59	0.58
FIV	0.13	0.22	0.35	0.49	0.45	0.40
FIM	0.20	0.27	0.31	0.56	0.56	0.47
RFI	0.27	0.41	0.42	0.58	0.59	0.58
FID	0.09	0.14	0.29	0.20	0.21	0.35

In Table 4 repeatabilities are given of feed intake characteristics. Repeatabilities were determined within two-week periods, within months and within the fattening period. Generally, in individual housing feed intake traits had a higher repeatability than in group housing, especially feed intake traits per meal. Repeatabilities estimated within short periods were higher than estimated within the whole fattening period. Rate of feed intake (RFI) and also number of visits and meals per day (NVD and NMD) were relative highly repeatable traits.

In Table 5 relationships between feed intake traits are presented. In both housing systems, but especially in group housing, correlations between feed intake and eating time per visit and per meal (FIV and FIM, TV and TM, FIV and TV and FIM and TM) were high. Rate of feed intake was negatively correlated with daily eating time (TD) and in individual housing RFI was strongly positively correlated with daily feed intake (FID). In individual housing, correlations between number of visits and number of meals (NLX, NVD and NMD) were lower than in group housing. After discarding extreme values to obtain normally distributed traits, correlations were estimated again.

In group housing correlations were not greatly influenced by omission of extreme values (14 of 229 records). In individual housing correlations were influenced by omission of 3 of 30 records.

TABLE 5. Correlation coefficients between feed intake traits estimated within housing system.

	FIM	FIV	TM	TV	RFI	TD	FID	NMD	NVD	NLX	TDLX	FILX
Group housing												
FIM	1.00											
FIV	0.91	1.00										
TM	0.81	0.71	1.00									
TV	0.78	0.87	0.90	1.00								
RFI	0.25	0.25	-0.34	-0.23	1.00							
TD	-0.02	-0.16	0.39	0.17	-0.66	1.00						
FID	0.22	0.03	0.12	-0.06	0.17	0.59	1.00					
NMD	-0.74	-0.76	-0.63	-0.69	-0.17	0.40	0.37	1.00				
NVD	-0.59	-0.76	-0.46	-0.68	-0.20	0.50	0.48	0.89	1.00			
NLX	-0.66	-0.58	-0.56	-0.51	-0.15	0.27	0.19	0.83	0.65	1.00		
TDLX	-0.06	-0.22	0.27	0.05	-0.51	0.85	0.57	0.39	0.48	0.22	1.00	
FILX	0.06	-0.13	-0.02	-0.20	0.16	0.41	0.76	0.34	0.44	0.10	0.74	1.00
Individual housing												
	FIM	FIV	TM	TV	RFI	TD	FID	NMD	NVD	NLX	TDLX	FILX
FIM	1.00											
FIV	0.77	1.00										
TM	0.69	0.61	1.00									
TV	0.54	0.82	0.83	1.00								
RFI	0.39	0.17	-0.36	-0.39	1.00							
TD	-0.21	-0.11	0.51	0.44	-0.84	1.00						
FID	0.50	0.18	-0.09	-0.22	0.81	-0.44	1.00					
NMD	-0.82	-0.66	-0.80	-0.62	-0.04	-0.01	-0.11	1.00				
NVD	-0.43	-0.82	-0.54	-0.85	0.20	-0.13	0.20	0.58	1.00			
NLX	-0.41	-0.32	-0.50	-0.37	0.03	-0.11	-0.02	0.57	0.32	1.00		
TDLX	-0.07	-0.02	0.58	0.48	-0.77	0.92	-0.38	-0.16	-0.19	0.09	1.00	
FILX	0.48	0.17	-0.13	-0.24	0.81	-0.47	0.96	-0.07	0.21	0.19	-0.34	1.00

DISCUSSION

From the distribution of visits during the day (Figure 1) it is shown that some could be grouped together into meals (especially for individually housed pigs) (see also Wiepkema, 1968). By plotting survival curves it was tried to determine the breakpoint by eye as effected by Salden and Sas (1976), but because the method was not objective as it was difficult to detect a clear breakpoint in the curve.

In literature, values for m.c. are reported for different species. By plotting survival curves of intervals between visits, Salden and Sas (1976) estimated m.c. of 2 to 16 minutes for different pigs housed individually, with an average value of 8.5 minutes. Bigelow and Houpt (1988) reported a minimum inter-meal interval of 10 minutes for individually housed young pigs. Strubbe and Gorissen (1980) chose a value of 15 minutes from a range of 10 to 40 minutes in lactating rats fed ad libitum. Metz (1975) reported a m.c. for cattle of 20 minutes. Ho and Chin (1988) arbitrarily chose a m.c. of 12 minutes for genetically obese mice. Also for mice, Wiepkema (1968) estimated a m.c. of five minutes. The average m.c. values that were found in this study by approximating survival curves with two polynomials did not differ greatly between the two housing systems. From the results five minutes was chosen as a general m.c. for both housing systems. One m.c. makes it possible to compare feed intake traits across housing systems. A m.c. was chosen that was equal to the estimated m.c. in group housing data, because in future research in particular feed intake patterns in group housing will be analysed. This m.c. falls within the range reported by Salden and Sas (1976) for individually housed pigs, but no comparison could be made with m.c. estimated for growing pigs housed in groups.

Pigs housed in groups generally ate less feed per day in less meals and less total time per day, compared with individually housed pigs. On the other hand, group housed pigs ate faster and had a larger feed intake per meal. The hypothesis is that this is caused by social interactions: a pig in a group has to eat fast to get enough feed because of competition with other pigs. Pigs in individual pens are less influenced by other pigs (only by sounds). Feed intake traits as eating time and feed intake per visit, meal and day (TV, FIV, TM, FIM, TD and FID) in group housing were slightly lower than reported in literature, whereas number of meals and visits per day (NMD, NVD) and rate of feed intake (RFI) were slightly higher or equal to values in literature (Bigelow and Houpt, 1987; Király et al., 1986; Schouten, 1986). Lower FIM, FIV and FID can be due to the breed. The larger number of meals and visits per day will reduce TV, FIV, TM and FIM when FID is equal. Further, TV, TM and TD could also be reduced because feed intake was lower and RFI was higher. The larger number of visits and meals compared with other reports in the literature could be explained by the continuous recordings and unrestricted access to the feeder (except when an other pig was present). In other investigations animals often had to press panel switches several times to be counted as a meal or registrations were performed every two or three minutes (Bigelow and Houpt, 1988; Duncan et al., 1970; Schouten, 1986).

In individual housing the number of meals was reduced considerably by using the Linda-index to determine the meals of major importance. In group housing the effect was smaller. This means that pigs in individual pens have, apart from a few large meals, many small meals with low RFI. Possibly they visit the feed hopper often as a pastime. In group housing pigs will not have many small meals on a day, because of competition.

The pattern of daily feed intake can be characterised by two peaks: a relatively smaller peak in the morning compared with and a large peak in the beginning of the afternoon, especially for group housed pigs. Similar results were found by Schouten (1986) and Marx et al. (1987). Pigs started eating around 6.00h. This is the time personnel of the farm started to work in the building. Individually housed pigs had a more even distribution of feed intake during the day, probably due to lack of competition for the feed and as they see no other pigs eating, through less stimulation to eat.

Feed intake per day, feed intake per day in the largest meals and rate of feed intake were normally distributed traits. Most traits had a positive kurtosis. A high positive kurtosis is due to long-tailed distributions. This means that there is much variation and there are extreme values, which should be examined carefully. For breeding purposes extreme values are interesting, but only if these values have a genetic background. Extremes due to measurement errors should be discarded. In both housing systems discarding of extreme values resulted in not significantly non-normal distributions, except for FIM, FIV, TM and TV. Traits per visit or per meal had skewed distributions and positive kurtosis. In group housing a logarithmic transformation could be used for these traits to obtain a normal distribution, but in individual housing this did not result in a normal distribution. The distribution of feed intake traits in individual housing was probably influenced by the small data set. In both housing systems discarding of extreme values did not greatly influence relationships. To investigate relationships between feed intake traits, more data than available in this experiment would be desirable to test normal distributions. Transformations to obtain normally distributed traits may be necessary, although the interpretation of the results will be more difficult.

Averages of estimated repeatabilities within two-week periods were higher than average repeatabilities within months or within the whole test period. Low repeatabilities indicate that much accuracy will be gained from multiple estimations and that it is difficult to predict future performance from past records. The repeatability also indicates the upper limit for the estimation of heritability. High repeatabilities were found for RFI and NMD in both housing systems. This means that observations on these traits during a short period will give much information about the average value during the total test period and that accuracy is not greatly improved by recording these traits during the whole fattening period. Repeatabilities estimated within individual housing were higher. As no competition for feed was present the feed intake pattern of individually housed animals was probably less influenced by the environment. Consequently, the special environmental variance which influences the variance component within animals σ^2_{wa} was smaller.

The manner of ingestion like frequency of eating or feed intake per meal may be related to the metabolism and nutritional status through enzymatic and endocrine activities. Cohn et al. (1962) found with full-spaced meals (meal eating) an increased body fat, decreased body protein and water, an increased urinary nitrogen excretion and higher feed to gain ratio compared with frequent small meals (nibbling). Foster et al. (1983) reported that with few but large meals per day pigs spent less energy on feed intake behaviour and were energetically more efficient. In future studies correlations between feed intake characteristics and production traits will be estimated.

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REFERENCES

Beasley, J.D. and Springer, S.G., 1977. Algorithm AS 111. The percentage points of the normal distribution. Appl. Stat., 26: 118-121.

Bergström, P.L. and Kroeske, D., 1968. Methods of carcass assessment in research on carcass quality in the Netherlands. I. Description of the methods. Annual EAAP Meeting, Dublin. Report, Institute for Animal Production, Zeist, C-123.

Bigelow, J.A. and Houpt, T.R., 1988. Feeding and drinking patterns in young pigs. Physiol. & Behav., 43: 99-109.

Cohn, C., Joseph, D. and Allweiss, M.D., 1962. Nutritional effects of feeding frequency. Am. J. Clinic. Nutr., 11: 356-361.

De Haer, L.C.M., Merks, J.W.M., Kooper, H.G., Buiting, G.A.J. and Van Hattum, J.A., 1992. The IVOG®-station: a feeding station to record the individual feed intake of group housed growing pigs. Anim. Prod., 54 (in press).

Duncan, I.J.H., Horne, A.R., Hughes, B.O. and Wood-Gush, D.G.M., 1970. The pattern of feed intake in female brown leghorn fowls as recorded in a Skinner box. Anim. Behav., 18: 245-255.

Foster, W.H., Kilpatrick, D.J. and Heaney, I.H., 1983. Genetic variation in the efficiency of energy utilization by the fattening pig. Anim. Prod., 37: 387-393.

Genstat 5 Committee, 1987. Genstat 5 Reference Manual. Oxford University press, Great Britain.

Harvey, W.R., 1977. User's guide for LSML76 (Mixed Model Least Squares and Maximum Likelihood Computer Program). Mimeo, Ohio State Univ., 76 pages.

Hill, I.D., 1973. Algorithm AS 66. The normal integral. Appl. Stat., 22: 424-427.

Ho, A. and Chin, A., 1988. Circadian feeding and drinking patterns of genetically obese mice fed solid chow diet. Physiol. & Behav., 43: 651-656.

Jong, H.W., de, 1985. Dynamische markttheorie. Stenferd Kroese B.V., Leiden, The Netherlands, pp. 23-24.

Király, A., Papp, J. and Wittmann, M., 1986. Effect of environmental factors on the behaviour of the fattening pigs. Int. Symposium on Applied Animal Behaviour, Balatonfüred, Hungary.

Marx, D., Buchholz, M. und Mertz, R., 1987. Beziehungen zwischen haltungstechnik und tagesrhythmus bei frühabgesetzten ferkeln. Aktuelle arbeiten zur artgemaessen tierhaltung, Freiburg. KBTL-schrift 323, pp. 9-35.

Merks, J.W.M., 1989. Genotype x environment interactions in pig breeding programmes. VI. Genetic relations between performances in central test, on-farm test and commercial fattening. Livest. Prod. Sci., 22: 325-339.

Metz, J.H.M., 1975. Time patterns of feeding and rumination in domestic cattle. Thesis Wageningen Agricultural University, The Netherlands, 75-12, pp. 214.

Royston, J.P., 1982a. An extension of Shapiro and Wilk's W test for normality to large samples. Appl. Stat., 31: 115-124.

Royston, J.P., 1982b. Algorithm AS 177. Expected normal order statistics (exact and approximate). Appl. Stat., 31: 161-165.

Royston, J.P., 1982c. Algorithm AS 181. The W test for normality. Appl. Stat., 31: 176-180.

Salden, N.T.C.J. and Sas, A.H.M., 1976. De groei en het niveau en tijdspatroon van de voeropname van ad libitum gevoerde HC-gevoelige en MHS-ongevoelige varkens. Student thesis, Wageningen Agricultural University, The Netherlands.

Schouten, W.G.P., 1986. Rearing conditions and behaviour in pigs. Thesis Wageningen Agricultural University, The Netherlands, pp. 54-71.

Shapiro, S.S. and Wilk, M.B., 1965. An analysis of variance test for normality. Biometrika, 52: 591-611.

Strubbe, J.H. and Gorissen, J., 1980. Meal patterning in the lactating rat. Physiol. & Behav., 25: 775-777.

Wiepkema, P.R., 1968. Behaviour changes in CBA mice as a result of one goldthioglucose injection. Behav., 32: 179-210.

Chapter 3

FEED INTAKE PATTERNS AND FEED DIGESTIBILITY OF GROWING PIGS HOUSED INDIVIDUALLY OR IN GROUPS

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L.C.M. de Haer and A.G. De Vries

ABSTRACT

In two batches with 10 individually housed pigs and 80 group housed pigs each, animals were tested for growth performance from ± 25 kg to 100 kg live weight. Ad libitum feed intake and feed intake pattern were recorded individually using IVOG®-stations. Digestibility coefficients for dry matter (DCdm) and crude protein (DCcp) in feed were determined. In the first batch only the 10 individually housed pigs were sampled, in the second batch all individually housed and group housed pigs were sampled. Digestibility was calculated as the average of two measurements.

Batch effect in individual housing was significant ($P<0.01$) for DCcp and DCdm. DCdm in individual housing was significantly higher ($P<0.01$) than in group housing. Sex effect and age at sampling were not significant for DCcp and DCdm across housing systems.

Group housed pigs had a significantly ($P<0.01$) lower growth rate and less backfat than individually housed pigs, whereas daily feed intake and feed conversion were not significantly different ($P>0.05$). Housing system had a significant influence ($P<0.05$) on feed intake pattern.

In both housing systems digestibility coefficients were positively correlated with growth rate and negatively correlated with feed conversion. In group housing the correlation of number of large meals per day with digestibility coefficients was significantly positive ($P<0.05$). Proportionately more large meals per day (group housing) and more visits within a meal (both housing systems) were positively related with DCdm. In individual housing better digestibility coefficients were related with more, short visits per day, an optimum rate of feed intake, less eating time per day and proportionately more eating time in large meals.

INTRODUCTION

In pig breeding programmes, breeding boars and gilts are usually tested in individual housing, whereas commercial growing pigs are kept in groups. To prevent genotype x housing system interactions, testing of pigs should take place in groups. De Haer and Merks (1992) showed that the feed intake pattern of group housed pigs was significantly different from the feed intake pattern in individual housing.

Feed intake pattern may influence fat and lean growth in the pig through an effect on the utilisation of nutrients (Batterham and Bayley, 1989; Bhar and Katiyar, 1989; Cohn et al., 1962; Den Hartog et al., 1989; Fábry, 1967; Leveille, 1970, Leveille and Chakrabarty, 1968). Feeding frequency may influence amylase and lipase secretions (Hee et al., 1988) and the mobility pattern of the small intestine (Ruckebusch and Bueno, 1976).

The objective of this study is to determine the relationships of feed intake and feed intake pattern with digestibility coefficients for dry matter and crude protein and their consequences for growth and carcass composition.

Experiments were conducted with ad libitum fed growing pigs, housed individually or in groups. Individual feed intake as well as feed intake pattern were recorded. Digestibility coefficients were determined by using chromic oxide as a marker in the feed in combination with faeces sampling.

MATERIALS AND METHODS

Experimental design

From January 1989 till October 1989 data on digestibility and feed intake patterns were collected from Dutch Landrace pigs during two batches. In each batch 80 pigs were housed in 10 pens of 8 animals per pen and 10 pigs were housed individually. The pigs were fed ad libitum. To reduce variation in final weights, boars and gilts were housed in separate pens. In each batch and housing system, 6 pens consisted of boars and 4 pens consisted of gilts.

The test period started at a live weight between 25 to 35 kg, with little weight variation between pigs within a pen. In the second batch, pigs were weighed every two weeks. The test was finished when an average live weight of 100 kg per pen was reached. At the age of 170 ± 10 days, backfat thickness was measured ultrasonically and the pigs were weighed. At the end of the test live weight and lean percentage (IVO standard dissection method (Bergström and Kroeske, 1968) and Hennessy Grading Probe (Walstra, 1987)) were determined.

To record individual feed intake, each pen was equipped with an IVOG®-station (De Haer et al., 1992). The feeding station consisted of a single space feed hopper which was weighed continuously. At each visit of a pig to the feeder, time and weight of the feed at the beginning and at the end of the visit were recorded automatically, together with the animal identification number. The pigs were identified by active ear responders. An eating pig was standing mainly unprotected and could be chased away by other pigs, thus allowing competition for the food. The entrance to the hopper could be adjusted to the size of the pigs, in order to prevent two pigs from eating at the same time.

In the first batch data on digestibility were collected only from the individually housed pigs (10). In the second batch all individually and group housed pigs were involved in the experiment.

The foods supplied were commercial foods for growing pigs. The feed during the first weeks of test (starter food), on average 50 kg per pig in total, contained 9.4 MJ/kg Net energy and 182 g/kg crude protein. The feed supplied for growing pigs contained 9.1 MJ/kg Net energy, 168 g/kg crude protein, 59 g/kg crude fibre and 71 g/kg ash. Crude fat content was 45 g/kg.

Digestibility measurements

To estimate digestibility, the marker method is a good alternative to the classic method of total faeces collection and is more practical (Petry and Enders, 1974; Daccord, 1982). The marker method is independent of feed and faeces losses during sampling.

Chromic oxide (Cr_2O_3) was used as a marker. Before making pellets, the feed for growing pigs was mixed with 2 g Cr_2O_3 per kg (0.2%) at the beginning of the test. The feed was supplied two times in the test period, during 7 days. Within a batch the same feed was used during the two sampling periods. Faeces collection took place during one of the last two days of the seven day period, at several times in the morning and afternoon until at least 0.3 kg faeces per pig were collected. Age at first sampling was on average 133 days (60-70 kg), at the second sampling age was on average 182 days (90-110 kg) (first batch) or on average 161 days (80-95 kg) (second batch). For practical reasons two days were necessary to sample all pigs of one pen.

The feed and faeces were analysed for chromic oxide content, dry matter and crude protein. Chromic oxide content was determined by titration with potassium permanganate. After dry ashing of the sample, the ash was evaporated to dryness with an alkaline phosphate solution and glowed in a muffle furnace. The chromic oxide was converted into bichromate ($Cr_2O_7^{2-}$). The bichromate was mixed with sulphuric acid and reduced to chromic (Cr^{3+}) with a known amount of ferrous ammonium sulphate. The excess of ferrous ammonium sulphate was titrated back with potassium permanganate. The chromic oxide content was calculated from the difference of using permanganate for the sample and for a control with only ferrous ammonium sulphate. Based on concentration of the marker in feed and faeces, digestibility coefficients were calculated according to the following formula:

$$DC\,x = \left[1 - r \times \left[\frac{Cr\ in\ feed}{x\ in\ feed} \right] \times \left[\frac{x\ in\ faeces}{Cr\ in\ faeces} \right] \right] \times 100$$

where: x = nutrient (dry matter (dm) or crude protein (cp)); r = recovery of the chromic oxide; it is assumed that $r = 1$; *Cr in feed* = concentration of chromic oxide in the feed; *Cr in faeces* = concentration of chromic oxide in the faeces; *x in feed* = concentration of dm or cp in the feed; *x in faeces* = concentration of dm or cp in the faeces

As measure of digestion during the fattening period average digestibility coefficients for dm and cp (DCdm and DCcp) were calculated, based on measurements in the two sampling periods.

Feed intake pattern

The data collected with the IVOG-station were used to describe the feed intake pattern of each pig by using the following traits (De Haer and Merks, 1992) as:

TV = eating time per visit (min)
TM = eating time per meal (min)
TD = eating time per day (min)
TDLX = daily eating time in NLX meals of major importance (min)
NVD = number of visits per day
NMD = number of meals per day
NLX = number of meals of major importance (according to Linda-index)
FIV = feed intake per visit (g)
FIM = feed intake per meal (g)
RFI = rate of feed intake (g/min)
FID = feed intake per day (g)
FILX = daily feed intake in NLX meals of major importance (g)

For grouping visits to meals, a meal criterion of 5 minutes was used (De Haer and Merks, 1992). Two successive visits of the same pig, without an interrupting visit of another pig and with the second visit starting after an interval of less than 5 minutes, were considered as one meal. The Linda-index (De Jong, 1985; De Haer and Merks, 1992) was used to select those large meals in a day that made a major contribution to the daily feed intake.

Statistical analysis

Of all group housed and individually housed pigs, feed intake pattern and production traits were recorded. The data sets for digestibility coefficients in individual and group housing were based on different circumstances of measurement and different numbers of observations: in individual housing digestibility coefficients were determined during two batches and in group housing only during the second batch.

To determine whether housing system, batch, sex and interactions of these effects influenced feed intake traits and production traits, these traits were analysed with Least Squares analysis (Harvey, 1977) according to model 1 described below (without age as a covariable). Preliminary analysis within group housing showed that pen effect was not significant and, therefore, it was not included in the model. When digestibility coefficients were analysed, housing system x batch interaction was omitted from the model. Digestibility coefficients might be influenced by weight at sampling, but this weight was only known during the second batch. Therefore, age at sampling was included as a covariable in model 1.

$$Y_{ijkl} = \mu + S_i + H_j + B_k + S \times H_{ij} + S \times B_{ik} + H \times B_{jk} + bA_{ijkl} + e_{ijkl} \qquad \text{(model 1)}$$

where: Y_{ijkl} = average digestibility coefficient, production trait or feed intake trait; S_i = (fixed) sex effect (i=1,2); H_j = (fixed) housing system effect (j=1,2); B_k = (fixed) batch effect (k=1,2); SxH_{ij} = interaction between sex and housing system; SxB_{ik} = interaction between sex and batch; HxB_{jk} = interaction between housing system and batch; b = regression coefficient for age at sampling; A_{ijkl} = (covariable) age at sampling; e_{ijkl} = error

Extreme digestibility coefficients were discarded when the value for DCcp or DCdm was outside the range of mean ± 2 standard deviations.

Housing system had a significant effect on digestibility coefficients and many feed intake and production traits. Therefore, correlations and regressions with digestibility coefficients were analysed separately for individual and group housing data, after correction for significant effects (Genstat 5 Committee, 1987). The difference between two correlation coefficients, estimated within individual and group housing, was tested for significance. This test was performed after transformation of the two correlation coefficients to almost normally distributed quantities z (Snedecor and Cochran, 1980). Models, consisting of fixed effects and combinations of a maximum of five feed intake traits that explain variation in digestibility coefficients, were investigated with the procedure RSELECT (Genstat 5 Committee, 1987). The ratio of variance that is accounted for is given by the adjusted R^2, expressed as:

$$adj.R^2 = 1 - \frac{residual\ mean\ squares}{total\ mean\ squares}$$

RESULTS

Data of 28 group housed pigs (17.5%) and 3 individually housed pigs (15%) were not used for analysis (Table 1). Nine group housed pigs finished the test prematurely, the other pigs had also suffered from health problems and, therefore, one or more digestibility coefficients or production traits were not measured or had extreme values.

Effects on digestibility coefficients

Analyses with model 1 showed a significant housing system effect for DCdm ($P<0.01$) (Table 1). In group housing DCdm was 70.7 and in individual housing DCdm was 73.2. Sex effect was not significant for DCdm and DCcp. Batch effect was significant for DCcp and DCdm ($P<0.01$) within individual housing data. Sex x housing system interaction was significant ($P<0.05$) for DCcp, indicating in individual housing higher DCcp values for gilts compared with boars and in group housing higher DCcp values for boars compared with gilts. Sex x batch interaction and effect of age at sampling were not significant for DCcp and DCdm.

TABLE 1. Least squares means and residual standard deviations of digestibility coefficients and production traits. Probabilities of housing system (H), sex (S) and batch (B) are given from analyses with model 1.

	Group housing	Individual housing	error st.d.	S	B	H
Digestibility coefficients						
Number of animals	62	17				
DC dry matter	70.7	73.3	1.89		**	**
DC crude protein	68.9	69.9	2.61		**	
Production traits						
Number of animals	132	17				
Growth rate (g/d)	642.3	741.9	71.9	**		**
Feed conversion	3.17	2.98	0.36	**		
Backfat thickness (mm)	12.2	13.8	1.7		**	**
HGP lean %	51.4	52.3	2.59			
IVO lean %	58.6	59.1	2.32		*	
Feed intake (g/d)	1934	2075	274			

probabilities:
* = $P < 0.05$
** = $P < 0.01$

Effects on production traits and feed intake pattern

Least squares means of production traits are presented in Table 1. Housing system had a significant ($P<0.01$) effect on growth rate during test and on backfat thickness. Growth rate and backfat thickness were higher for individually housed pigs. A significant sex effect ($P<0.01$) was found for growth rate and feed conversion. Interactions were not significant.

TABLE 2. Least squares means and residual standard deviations of feed intake traits. Probabilities of sex (S), batch (B) and housing system effect (H) are given from analyses with model 1.

	Group housing	Individual housing	st.d.	S	B	H
Time/visit (TV) (min)	4.76	1.38	1.46			**
Time/meal (TM) (min)	6.85	4.02	1.77	*		**
Time/day (TD) (min/d)	62.5	83.2	12.7			**
Time/day in large meals (min/d) (TDLX)	52.8	66.5	12.2		**	**
No. visits/day (NVD)	16.2	72.8	7.4	**	*	**
No. meals/day (NMD)	10.3	22.9	2.6	**		**
No. large meals/day (NLX)	6.28	8.42	1.79	**	**	**
Feed intake/visit (FIV) (g)	155.8	34.9	47.5			**
Feed intake/meal (FIM) (g)	223.8	103.6	54.9			**
Rate of feed intake (RFI) (g/min)	32.4	26.9	4.7			**
Feed intake/day (FID) (g/d)	1934	2075	274			
Feed intake/day in large meals (FILX) (g/d)	1696	1876	340			*

probabilities:
* = $P < 0.05$
** = $P < 0.01$

Feed intake patterns in individual and group housing are shown in Table 2. Housing system always had a significant influence ($P<0.05$) on feed intake traits, except for daily feed intake. In group housing eating time per meal, feed intake per meal and rate of feed intake were higher. In individual housing pigs had more visits and meals and more eating time per day compared with pigs in group housing. TM, NVD, NMD and NLX were significantly influenced by sex. Boars had less visits and meals per day, but they had a higher eating time per meal compared with gilts. Sex x housing system interaction was significant for the mutually correlated traits NVD, NMD ($P<0.01$) and NLX ($P<0.05$), indicating that sex differences within group housing were rather small, but in both housing systems gilts had a higher frequency of eating than boars. As SxH interaction was only present for frequency of eating, correlations and regressions were not corrected for this effect. SxB and BxH interactions were not significant.

Relationships between digestibility and feed intake pattern

Correlations of feed intake traits and production traits with digestibility coefficients were estimated within group housing data and individual housing data, after correction for sex, batch and housing system effects.

TABLE 3. Phenotypic correlations of average digestibility coefficients for dry matter (DCdm) and crude protein (DCcp) with feed intake traits. Correlations are estimated within group housing data and individual housing data after correction for sex, housing system and batch effect. Significance of difference between correlations, estimated in two housing systems, is indicated in the last two columns.

	Group housing		Individual housing		Difference of correlations	
	DCdm	DCcp	DCdm	DCcp	DCdm	DCcp
Time/visit (TV)	-0.11	-0.09	-0.59*	-0.60*		*
Time/meal (TM)	-0.05	-0.09	-0.37	-0.40		
Time/day (TD)	0.01	-0.06	-0.71**	-0.64**	**	*
Time/day in large meals (TDLX)	0.03	-0.06	-0.75**	-0.69**	**	*
No. visits/day (NVD)	0.22	0.16	0.56*	0.72**		*
No. meals/day (NMD)	0.12	0.10	-0.01	0.16		
No. large meals/day (NLX)	0.28*	0.35**	-0.12	0.03		
Feed intake/visit (FIV)	-0.08	-0.03	-0.22	-0.24		
Feed intake/meal (FIM)	-0.03	-0.03	0.12	0.05		
Rate of feed intake (RFI)	0.05	0.13	0.54*	0.47		
Feed intake/day (FID)	0.05	0.04	0.28	0.26		
Feed intake/day in large meals (FILX)	0.03	-0.04	0.37	0.37		

probabilities:
* = $P < 0.05$
** = $P < 0.01$

In group housing an increased frequency of eating (NVD, NMD, NLX) was positively correlated with digestibility coefficients (Table 3). Only the correlation between number of large meals per day and digestibility coefficients was significant ($P<0.05$). In data collected in individual housing, more visits per day, less eating time per visit and per day and a higher rate of feed intake were significantly correlated ($P<0.05$) with higher digestibility coefficients. Daily feed intake was positively, though not significantly, correlated with digestibility.

Significantly different correlations between the two housing systems were found for TV, TD, TDLX and NVD with DCcp ($P<0.05$) and for TD and TDLX with DCdm ($P<0.01$). This indicates a lower linear relationship with digestibility, and possibly a greater variability for these feed intake traits, within group housing compared to individual housing.

In Table 4 models are presented that explained variation in DCdm by using different combinations of feed intake traits, corrected for fixed effects. Explained variance ratios (adj.R^2) for DCdm and DCcp were comparable, therefore only results for DCdm are presented.

Due to low correlations, in group housing little variation in digestibility between animals can be explained by feed intake pattern. Models with traits describing eating frequency (NVD, NMD, NLX) explained variation in digestibility coefficients best. The model with NVD, NMD and NLX explained 19% of the variation in DCdm in group housing and 20% when TD was added. Regression coefficients indicate that when relatively more visits are present at a constant number of meals, or when relatively more large meals are present, DCdm will increase. The model with covariables RFI and RFI^2 did not explain variation in DCdm, therefore an optimum rate of feed intake was not estimated.

In individual housing the model with TD, NVD, NMD and NLX explained 81% of the variation in DCdm and 86% when TDLX was added. In these models, regression coefficients indicate a higher DCdm when proportionately more visits within a large meal are present, or when proportionately more eating time is spent in large meals. An optimum average rate of feed intake during test of 28 g/min could be derived from estimated regression coefficients for RFI and RFI^2.

TABLE 4. Partial regression coefficients and adjusted R^2 of models, explaining variation in digestibility coefficients for dry matter with alternative covariables describing the feed intake pattern. Regression coefficients were adjusted for sex, housing system and batch effect.

Group housing

NMD	NVD	NLX	TM	TD	TDLX	FID	RFI	RFI^2	**adj.R^2**
		0.28*							0.06*
-0.20		0.49*							0.07*
		0.50**	0.35	-0.03					0.08
-0.87**	0.27**	0.73**							0.19**
-0.91**	0.34**	0.71**				-1.29	0.05		0.19**
-0.88**	0.31**	0.70**		-0.02					0.20**
-0.62	0.31**	0.68**	0.36	-0.06					0.20**

Individual housing

NMD	NVD	NLX	TM	TD	TDLX	FID	RFI	RFI^2	**adj.R^2**
							1.12*	-0.02	0.45**
				-0.10**					0.47**
					-0.13**				0.53**
	0.05**				-0.12**				0.68**
	0.06**			-0.09**					0.72**
-0.11	0.07**				-0.09**				0.76**
-0.01	0.03**	-0.22**		-0.10**					0.81**
	0.06**	-0.23**		-0.10**					0.83**
	0.07**	-0.27**		-0.15**	0.07				0.83**
	0.07**	-0.36**	-0.33	-0.19**	0.13				0.83**
0.23	0.06**	-0.59**		-0.30*	0.24*				0.86**

probabilities:

* = $P < 0.05$;

** = $P < 0.01$

Relationships between digestibility and production traits

In both housing systems correlations between digestibility coefficients and production traits were not significant (Table 5). Correlations of digestibility coefficients with growth rate were positive, the correlations with feed conversion were negative. In data obtained with individual housing of animals, correlations of digestibility coefficients with daily feed intake and backfat thickness were positive. Correlations were not significantly different between two housing systems.

TABLE 5. Phenotypic correlations of average digestibility coefficients for dry matter (DCdm) and crude protein (DCcp) with production traits in two housing systems. Correlations are estimated after correction for sex, housing system and batch effect.

	Group housing		Individual housing	
	DCdm	DCcp	DCdm	DCcp
Growth rate	0.22	0.23	0.35	0.33
Feed conversion	-0.13	-0.17	-0.37	-0.41
Backfat thickness	0.14	0.12	0.37	0.30
HGP lean %	-0.04	0.06	-0.06	0.09
IVO lean %	0.00	0.06	-0.15	-0.01
Feed intake/day	0.05	0.04	0.28	0.26

probabilities:
* = $P < 0.05$
** = $P < 0.01$

DISCUSSION

Effects on digestibility coefficients

Digestibility of nutrients in feed depends on composition of the diet and animal characteristics (Wenk, 1983). Digestibility coefficients with the feeds and animals reported in literature (Daccord, 1982; Elbers et al., 1989; Häller, 1989; Petry and Enders, 1974; Wenk and Morel, 1985; Wilmink, 1979) are normally slightly higher than obtained with the feed and animals in this experiment. Crude fibre content of the feed was relatively low (59.5 g/kg). Low digestibility coefficients in both housing systems could be due to environmental factors like climate and feeding strategy: ad libitum feeding may reduce digestibility (Wenk and Morel, 1985). Unequal distribution of chromic oxide through the feed or an incomplete recovery of chromic oxide could also have influenced the digestibility coefficients. Also, genotype may have affected digestibility. The pigs in this experiment were offspring from a line of Dutch Landrace pigs that had not been selected for high growth rate and leanness during seven generations (Merks et al., 1986). Coefficients of variation (CV) for digestibility coefficients were very low (2 to 4%), probably due to their representation as a fraction and because they represented average values of two measurements.

Correlations between digestibility coefficients in the two sampling periods were lower in group housing than in individual housing. This indicates a lower repeatability of digestibility measurements in group housing. Lower repeatabilities could be caused by social interactions in group housing (De Haer and Merks, 1992), since interactions increase within animal variation.

Age did not have a significant influence on DCdm and DCcp. Average digestibility coefficients based on two measurements were used as observations. The average age at sampling did not differ much between animals (maximum age difference was 24 days). DCdm was significantly lower for group housed pigs than for individually housed pigs. This is comparable to results found by Oude Elferink et al. (1986). Sex effect was not significant, in agreement with Häller (1989), Wenk and Morel (1985) (differences between gilts and barrows) and Siers (1975) (gilts, boars and barrows). Wilmink (1979), however, found a significantly better DCcp for gilts compared with barrows.

Effects on production traits and feed intake pattern

Housing system had a significant influence on growth rate, backfat thickness, and most feed intake traits. The lower growth rate and backfat thickness in group pens can be explained by a lower daily feed intake (not significant), a lower digestibility and a higher level of activity due to social interactions. Social interactions also influenced feed intake pattern. As was already reported by De Haer and Merks (1992), pigs housed in groups had less meals per day, but meal size and eating time per meal were higher. Rate of feed intake was also higher. On a daily basis however, group housed pigs had a slightly lower feed intake and spent less time eating.

Relationships between digestibility and feed intake pattern

The digestion of the feed depends on the rate of feed passage through the gut and the amount of intestinal enzyme production. The rate of passage determines the time of contact between feed and enzymes and the time of contact between digestion products and absorptive surfaces (Rérat and Corring, 1991). Pigs with many meals of limited size will have a more continuous flow of digesta through the intestine (Ruckebusch and Bueno, 1976; Sissons and Jones, 1991) and an increased amylase production, whereas lipase secretion is reduced (Hee et al., 1988). Xu et al. (1991) reported an increased gastrin production when total eating time per day is lower and feed intake per meal and per minute are higher. These results suggest that there is an influence of feed intake pattern on the digestive capacity of the pig.

In group housing an increased number of large meals had a positive relation with digestibility coefficients. When relatively more visits were present within a meal, or relatively more large meals were present, digestibility was positively influenced. This indicates that eating with many, relatively small, portions within a meal has a positive influence on the digestibility. At equal levels of daily feed intake an increase in number of meals per day will provide a more balanced supply of essential amino acids, resulting in a better utilisation of amino acids (Batterham and Bayley, 1989; Bhar and Katiyar, 1989; Cohn et al., 1962; Den Hartog et al., 1989; Fábry, 1967).

In individual housing the significant correlations between feed intake pattern and digestibility coefficients were partly influenced by the positive relation between daily feed intake and digestibility, but this relation was not significant. Pigs with many visits of short duration, with an optimum rate of feed intake and with a low daily eating time had significantly better digestibility coefficients. Proportionately more visits within a large meal and proportionately more eating time in large meals had a positive relation with digestibility. Correlations with TD and RFI indicate that rate of feed intake is more important in individual housing than in group housing, probably due to the lower rate of feed intake. Variation in RFI is due to variation in number of bites and size of the bites when a pig stands at the feed hopper, but also variation in waiting periods (when no feed is consumed) during feed intake recording plays a role. An optimum RFI indicates that at a certain rate of feed intake the digesta is propagated too fast through the digestive tract to ensure enough contact with enzymes and the absorptive surface. As enzyme production is dependent on meal size (Hee et al., 1988; Xu et al., 1991), digestion may also not be optimal at a very low RFI.

Correlations of digestibility coefficients with NVD, TD, TDLX and TV were significantly ($P < 0.05$) influenced by housing system. If feed intake pattern is genetically determined, this effect may cause genotype x housing system interactions.

Relationships between digestibility and production traits

At constant live weight an increase in daily feed intake will usually result in lower digestibility coefficients (Elbers et al., 1989; Oude Elferink et al., 1986). In individual housing, however, a positive correlation was found between daily feed intake and digestibility coefficients, independent of age. This was partly due to differences in live weight since correction for age did not take away all variation due to differences in pig size. Digestibility increases with increasing pig size (Siers, 1975; Wenk, 1973; Wenk and Morel, 1985). It was not clear whether better digestibility caused a higher daily feed intake and bigger pigs or that a high daily feed intake resulted in bigger pigs that could digest the feed better. Variation in daily feed intake can be a consequence or a cause of variation in digestibility of the food. Therefore, correlations between feed intake pattern and digestibility coefficients were not corrected for daily feed intake. Another reason was that production traits were influenced by average daily feed intake during test, whereas digestibility coefficients were influenced by daily feed intake during sampling. Correction of digestibility and production traits with the same variable would therefore not be appropriate.

In both housing systems an increase in digestibility was related to a higher growth rate and better feed conversion (Table 4). In individual housing digestibility coefficients were also positively correlated with backfat thickness, but this relationship could be due to the positive correlation of digestibility with daily feed intake. The positive relation between growth rate and digestibility was also reported by Wenk and Morel (1985) (ad libitum feeding and restricted feeding, individual housing of pigs) and Wilmink (1979) (ad libitum feeding, group housing), who also found a lower feed conversion when digestibility coefficients were increased. Higher digestibility coefficients for pigs selected for backfat thickness compared with pigs selected for lean growth was reported by Sundstøl e.a. (1979).

Conclusions

From the results it can be concluded that, especially in individual housing, correlations exist between feed intake pattern and digestibility coefficients. Proportionately more visits per meal was positively related with DCdm. In group housing higher digestibility coefficients were correlated with many large meals. In individual housing higher digestibility coefficients were correlated with more visits per day, an optimum rate of feed intake and a low daily eating time with proportionately more eating time in large meals. In both housing systems better digestibility coefficients were correlated with a higher growth rate and an improved feed conversion.

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REFERENCES

Bhar, R. and Katiyar, R.C., 1989. Effect of frequency of feeding on the efficiency of protein utilization of cattle. Ind. J. Anim. Nutr., 6(2):126-131.

Batterham, E.S. and Bayley, H.S., 1989. Effect of frequency of feeding of diets containing free or protein bound lysine on the oxidation of [^{14}C]lysine or [^{14}C]phenylalanine by growing pigs. Br. J. Nutr., 62: 647-655.

Bergström, P.L. and Kroeske, D., 1968. Methods of carcass assessment in research on carcass quality in the Netherlands. I. Description of the methods. EAAP meeting Dublin; IVO-report C-123, Zeist, The Netherlands.

Cohn, C.M.D., Joseph, D. and Allweiss, M.D., 1962. Nutritional effects of feeding frequency. Am. J. Clinic. Nutr., 11:356-361.

Daccord, R., 1982. Comparaison de l'oxide de chrome et des cendres insolubles dans HCl utilisés comme marqueurs dans des essais de digestibilité chez le porc. Recherche Agronomique en Suisse, 21(3/4):159-165.

De Haer, L.C.M. and Merks, J.W.M., 1992. Patterns of daily feed intake in growing pigs. Anim. Prod., 54 (in press).

De Haer, L.C.M., Merks, J.W.M., Kooper, H.G. and Van Hattum, J.A. van, 1992. A note on the IVOG®-station: a feeding station to record the individual feed intake of group housed growing pigs. Anim. Prod., 54 (in press).

De Jong, H.W., 1985. Dynamische Markttheorie. Stenferd Kroese B.V., Leiden, The Netherlands, pp. 23-24.

Den Hartog, L.A., Verstegen, M.W.A. and Huisman, J., 1989. Amino acid digestibility in pigs as affected by diet composition. In: Friedman, M. (Editor), Absorption and utilization of amino acids, Vol. III., CRC Press, Florida, pp. 201-216.

Elbers, A.R.W., Den Hartog, L.A., Verstegen, M.W.A. and Zandstra, T., 1989. Between- and within-herd variation in the digestibility of feed for growing-finishing pigs. Livest. Prod. Sci., 23:183-193.

Fábry, P., 1967. Metabolic consequences of the pattern of feed intake. In: Code, F.P. (Editor), Handbook of physiology, Sect. 6: Alimentary canal. American Physiological Society, pp. 31-49.

Genstat 5 Committee, 1987. Genstat 5 Reference Manual. Oxford University Press, Great Britain.

Häller, B.A., 1989. Betriebsbedingte variation in der verwertung der Nahrungs-Energie bei wachsenden schweinen. Thesis no. 8986, Institute for Animal Production, ETH, Zürich, Switzerland.

Harvey, W.R., 1977. User's guide for LSML76 (Mixed Model Least Squares and Maximum Likelihood Program). Mimeo, Ohio State University, 76 pages.

Hee, J., Sauer, W.C. and Mosenthin, R., 1988. The effect of feeding on the pancreatic secretions in the pig. J. Anim. Physiol. Anim. Nutr., 60:249-256.

Leveille, G.A., 1970. Adipose tissue metabolism: influence of periodicity of eating and diet composition. 53rd. Annual Meeting of the Federation of American Societies for Experimental Biology. Federation Proceedings, 29(3):1294-1301.

Leveille, G.A. and Chakrabarty, K., 1968. Absorption and utilization of glucose by meal-fed and nibbling rats. J. Nutr., 96:69-75.

Merks, J.W.M., Buiting, G.A.J. and Brascamp, E.W., 1986. A selection experiment on the interval weaning - first oestrus. I. Design of the experiment and the results of the first two generations. Contribution to the 37th Annual EAAP Meeting, Budapest, Hungary.

Oude Elferink, G., Mentink, A., Everts, H., Smits, B. and Jongbloed, A.W., 1986. Digestibility in swine depending on several factors: literature research and report of a number of trials. Report no. 174, IVVO, Lelystad, The Netherlands.

Petry, H. and Enders, H., 1974. Kritische Betrachtungen über die Zuverlässigkeit der im klassischen Verdauungsversuch und nach der Chromoxid-Indikatormethode bestimmten verdauungskoeffizienten. Zeitschrift für Tierphysiologie, Tierernährung und Futtermittelkunde, 33:88-98.

Rérat, A. and Corring, T., 1991. Animal factors affecting protein digestion and absorption. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Digestive physiology in pigs. Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ.no. 54, Pudoc, Wageningen, The Netherlands, pp. 5-34.

Ruckebusch, Y. and Bueno, L., 1976. The effect of feeding on the motility of the stomach and small intestine in the pig. Br. J. Nutr., 35:379-405.

Siers, D.G., 1975. Chromic oxide determined digestion coefficients and their relationship to rate of gain and feed efficiency in individually fed Yorkshire boars, barrows and gilts. J. Anim. Sci., 41(5):1266-1269.

Sissons, J.W. and Jones, C.L., 1991. Ultrasonic and electromyographic measurements of the effects of feed intake on digesta flow and gastro-intestinal motility in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no. 54, Pudoc,Wageningen, The Netherlands, pp. 120-125.

Snedecor, G.W. and Cochran, W.G., 1980. Statistical methods. The Iowa State university press, Ames, Iowa, U.S.A., pp. 185-188.

Sundstøl, F., Standal, N. and Vangen, O., 1979. Energy metabolism in lines of pigs selected for thickness of backfat and rate of gain. Acta Agric. Scand., 29:337-345.

Walstra, P., 1987. The instrumental classification and grading of pigs in the Netherlands. Workshop "Experiences in Europe about porc objective grading", Reggio Emilia, Italy.

Wenk, C., 1973. Einfluss verschieden hoher zufuhr von Futterenergie und Futterprotein auf den gesamtstoffwechsel, die Mastleistung und die Schlachtkörper-zusammensetzung wachsender schweine. Thesis no. 4973, Institute for Animal Production, ETH, Zürich, Switzerland.

Wenk, C., 1983. Zur Verwertung des Schweinefutter: Protein, Energie. In: Die Versorgung von wachsenden Schweinen und Geflügel mit Protein und Energie; Tagungsbericht Eidgenössische Technische Hochschule, Zürich. pp. 18-29.

Wenk, C. and Morel, P., 1985. Genetic variation of the digestibility of energy in growing pigs. Proceedings of the 3rd International Seminar on Digestive physiology in the pig, Copenhagen, Denmark. pp. 396-399.

Wilmink, H., 1979. Digestibility coefficients in lines of pigs selected for growth and backfat thickness. M.Sc. thesis, Dept. Anim. Breed., Agricultural University of Wageningen, The Netherlands.

Xu, R.-J., Cranwell, P.D. and Hennessy, D.P., 1991. Effects of method of feeding and meal size on the postprandial gastrin response in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no. 54, Pudoc, Wageningen, The Netherlands, pp. 41-46.

Chapter 4

RELATIONSHIPS BETWEEN INDIVIDUAL RESIDUAL FEED INTAKE AND FEED INTAKE PATTERN IN GROUP HOUSED GROWING PIGS

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L.C.M. de Haer, P. Luiting and H.L.M. Aarts

ABSTRACT

Individual daily feed intake (FID) and feed intake pattern were recorded on a total of 405 group housed growing pigs, divided over five batches. Residual feed intake (RFID) was defined as FID minus predicted feed intake (pFID) based on metabolic body weight (MBW) and production level (body weight gain and IVO lean percentage in the carcass). Variation in pFID accounted for 32% of the variation in FID.

Correlations between RFID and feed intake pattern traits were calculated to determine the effect of feed intake activity. Correlations of RFID with daily eating time and eating frequency were significantly positive. The relationships indicated that the more efficient pigs (with a low RFID) had less meals, with visits to the feed hopper more spread out over the day, and they spent less time eating per day. Furthermore, these pigs showed a slightly higher feed intake per visit. Variation in feed intake activity, described by number of visits per day and daily eating time, accounted for 47% of the variation in RFID.

Pigs with a higher pFID were pigs with a higher production level, represented by a higher daily weight gain and more backfat. There were no clear correlations between pFID and eating frequency or duration, but pigs with a higher pFID had a higher rate of feed intake and a higher feed intake per visit and per meal.

It is concluded that combination of a high production level with a low RFID (high production efficiency), is associated with a short daily eating time, a low eating frequency and high feed intake per visit.

INTRODUCTION

In pig breeding the concept of appetite (i.e. ad libitum feed intake) is very much used (Vangen and Kolstad, 1986). The discussion about this concept is mainly focused on the decline in appetite with traditional selection on daily gain and against backfat thickness. Also, the possible negative consequences of it in the long run are often discussed. To contribute to this discussion the trait 'residual feed intake' is introduced in the present paper.

Variation in feed intake among animals may be explained by variations in metabolic body weight and in production level. Therefore, the feed intake of an animal may be predicted from its metabolic body weight and from production level. The difference between observed feed intake and predicted feed intake is defined as residual feed intake (RFID; Luiting and Urff, 1987). In the case of growing pigs, production includes the amounts of body fat tissue and lean tissue deposited during test. The total is represented by body weight gain during test and parameters describing body fat and lean percentages (Luiting and Urff, 1987). Foster et al. (1983) estimated RFID from comparison of predicted feed intake based on metabolic body weight, body weight gain, a fat index and actual feed intake.

Variations in energetic efficiencies for maintenance and for protein and fat accretions, variation in feed digestibility and variation in maintenance requirements per metabolic kilogram are not accounted for in the prediction model. The latter variation includes physical activity, sustaining body temperature, maintenance of body tissues and basal metabolic rate. As a consequence, this variation will be part of RFID. These non-accounted energy costs may play important roles in variation of gross energy utilisation in pigs (Metz et al., 1980).

In laying hens RFID can be an adequate trait to measure individual maintenance requirements per kilogram metabolic body weight. It was shown that especially physical activity was highly positively correlated with RFID (Luiting et al., 1991). In laying hens, activity related heat production can amount 9 to 26% of the total heat production per day. Luiting (1991) also found clear differences in this trait between different genotypes. Eating activity seems to be responsible for a large part of that variation; heat production increased by 10 to 67% during eating, resulting in a daily increase in heat production of 1 to 22% (Luiting, 1991). Braastad and Katle (1989) also found a positive relation between feed intake activity and RFID.

In growing pigs activity related heat production can amount from 8% to 20% of the total heat production per day, depending on age and feeding level (Verstegen et al., 1982). For ad libitum fed piglets Halter et al. (1979) showed that activity increased total heat production by 10 to 17% and maintenance requirements by 18 to 25%. When piglets where fed restricted, activity related heat production showed proportionately more variation (10 to 28% of total heat production) and was on average 30% higher than when piglets were fed ad libitum (Halter et al., 1979). Thus, it may be expected that feed intake activities, like frequency, duration and rate of eating, will influence heat production. Relationships between feed intake activities and RFID have not been reported yet in pigs.

To investigate the individual daily feed intake of group housed pigs fed ad libitum, the IVOG®-station was developed (De Haer et al., 1992). This feeding station also records the individual feed intake pattern, like daily number of visits to the hopper, eating time and feed intake per visit, etc. The aim of the present study is to investigate the relations of feed intake pattern with daily feed intake, with production traits and with RFID.

MATERIAL AND METHODS

Experimental design

From September 1988 till May 1991 data were collected from five batches of group housed Dutch Landrace (DL) and Great Yorkshire (GY) pigs. During each of the first three batches, 80 DL pigs were housed in 10 pens with each 8 animals per pen. In each of the following two batches, DL and GY pigs were housed in 14 group pens for 8 pigs.

The test period started at a live weight between 25 to 35 kg. It was finished when the mean live weight per pen was at least 100 kg. Pigs were weighed at start and at the end of test. Daily weight gain during test (WG) was calculated. To reduce variation in end weight like under practical conditions, pigs were grouped together according to weight and each pen consisted of only boars or only gilts of one breed. Litter-mates were put in different pens as much as possible.

During test, at the age of 170 ± 10 days backfat thickness (BT) was measured ultrasonically on four points at the back, 5 cm beside the central line of the back. At the end of test, pigs were slaughtered and lean percentage in the carcass was measured by two methods: IVO standard dissection method (Bergström and Kroeske, 1968) and Hennessy Grading Probe (HGP) (Walstra, 1987). IVO lean percentage was calculated as the percentage of dissected ham + shoulder + loin + lean offal (defatted, but bone included) in the carcass. HGP measurements were based on the measurement of backfat thickness and muscle thickness (mm) at the third to fourth rib from the last rib position, 6 cm from the dorsal mid-line (3/4 LR). From a regression formula the lean percentage could be derived.

The pigs were fed ad libitum. To record individual feed intake and feed intake pattern, each pen was equipped with an IVOG-station (De Haer et al., 1992). The feeding station consisted of a feed hopper which was weighed continuously. At each visit of a pig to the feeder, time and weight of feed at the beginning and at the end of the visit were recorded automatically, together with the animal identification number. Competition for the feed was possible, as an eating pig was mainly unprotected during eating.

Feed supplied during the first weeks of test (total on average 50 kg per pig) contained 9.4 MJ Net Energy/kg and 182 g/kg crude protein. Feed supplied for growing pigs contained 9.1 MJ Net Energy/kg and 168 g/kg crude protein.

Residual Feed Intake

To calculate residual feed intake per day (RFID), the observed daily feed intake (FID) was adjusted for effects of batch, sex, breed, pen and covariables describing metabolic body weight and production level. Analysis was performed on traits expressed per day to account for variation in number of fattening days. The following model was applied:

$$
\begin{aligned}
FID_{ijklm} &= \mu + B_i + S_j + R_k + B\times S_{ij} + B\times R_{ik} + S\times R_{jk} + P_{l:ijk} + b_1 MBW_{ijklm} + \sum_{n=2}^{4}(b_n X_{ijklmn}) + e_{ijklm} \\
&= B_i + S_j + R_k + B\times S_{ij} + B\times R_{ik} + S\times R_{jk} + P_{l:ijk} + pFID_{ijklm} + RFID_{ijklm} \qquad (1)
\end{aligned}
$$

where: FID_{ijklm} = average daily feed intake during test (kg/d); μ = adjusted mean; B_i = batch effect (i=1,...5); S_j = sex effect (j=1,2); R = breed effect (k=1,2); BxS_{ij} = interaction effect between batch and sex; BxR_{ik} = interaction effect between batch and breed; SxR_{jk} = interaction effect between sex and breed; $P_{l:ijk}$ = pen effect nested within batch, sex and breed (l=1,...,6); MBW_{ijklm} = covariable describing metabolic body weight (kg$^{0.75}$); b_1, b_n = partial regression coefficients; X_{ijklmn} = covariables describing production level (n = 2...4); e_{ijklm} = error term

FID was corrected for fixed effects and their interactions, to estimate pFID and RFID independent of the fixed effects. pFID will only depend on variation in body composition and body weight, RFID represents the residual variation, pooled within breed, sex, batch and pen.

$$pFID_{ijklm} = \mu + b_1 MBW_{ijklm} + \sum_{n=2}^{4} (b_n X_{ijklmn})$$

= predicted daily feed intake (kg/d)

$$RFID_{ijklm} = e_{ijklm} = FID_{ijklm} - pFID_{ijklm} - (B_i + S_j + R_k + B \times S_{ij} + B \times R_{ik} + S \times R_{jk} + P_{l:ijk})$$

= residual daily feed intake (kg/d)

Metabolic body weight (MBW) was calculated analogous to Foster et al. (1983), assuming a linear increase in weight between start and end of test:

$$\begin{aligned} MBW &= \int_{t_0}^{t_1} W^{0.75} dt / (t_1 - t_0) \\ &= \int_{W_0}^{W_1} W^{0.75} dW (dt/dW) / (t_1 - t_0) \\ &= (t_1 - t_0)/(W_1 - W_0) \int_{W_0}^{W_1} W^{0.75} dW / (t_1 - t_0) \\ &= \frac{(W_1^{1.75} - W_0^{1.75})}{1.75 \times (W_1 - W_0)} \end{aligned} \tag{2}$$

where: *MBW* = metabolic body weight ($kg^{0.75}$); t = day of test (t_0 = start; t_1 = end); W = weight during test (kg; W_0 = weight at start; W_1 = weight at end)

A simple approximation for production level during test is daily weight gain (WG). This means that differences in body composition are not taken into account. Thus, an approach to account for these body composition differences would be to add traits describing body fat and lean percentages to the regression model. No data on body composition at start of test were available. Therefore, only body weight at start (W_0) was used. This seems justified, because the variation in body composition at the start is thought to be less than at the end. Data on body composition measurements at the end of test (IVO and HGP carcass lean percentages and BT ultrasonic backfat thickness) and weight at the end of test were used to describe fat and lean gain. Alternatively, the product of WG and some body composition measure may be a better approximation of lean and fat tissue formation than an additive combination of them. According to this, IVO lean percentage was chosen to calculate the following two traits: LEAN= (IVO) WG / 100

FAT = (100-IVO) WG /100.

Summarising, the following traits were used for X_{ijklmn} in model (1):

WG = daily weight gain (g/d)
IVO = IVO lean percentage in the carcass
HGP = HGP lean percentage in the carcass
BT = ultrasonic backfat thickness at 170 days of age (mm)
W_0 = weight at start of test (kg)
LEAN = approximated lean tissue formation (g/d)
FAT = approximated fat tissue formation (g/d)

With the directive RSELECT (Genstat 5 Committee, 1987) the best model was selected with regard to X_{ijklmn} (to a maximum of four traits; MBW included) based on adjusted R^2 and mean square error. Adjusted R^2 was calculated as:

$$adj.R^2 = 1 - \frac{residual\ mean\ squares}{total\ mean\ squares}$$

The distribution of RFID was evaluated by calculating skewness and kurtosis and by calculating the WILK-test (W-test) value for normality (Shapiro and Wilk, 1965).

Feed intake pattern

Visits recorded by the IVOG®-stations (De Haer et al., 1992) were used to describe individual feed intake pattern. To group visits into meals, a meal criterion of 5 minutes was used according to De Haer and Merks (1992). This means that two successive visits of a pig, the second starting within 5 minutes after the first and without a visit of another pig interrupting, were grouped together and considered as one meal. The Linda-index (De Haer and Merks, 1992) was used to select the large meals per day that have together a major contribution to the daily feed intake. As a consequence the following traits describing daily frequency, duration and rate of eating were considered:

TV = time per visit (min)
TM = time per meal (min)
TLX = TDLX/NLX = time per large meal (min)
TD = time per day eating (min)
TDLX = time per day in large meals (min)
TDLX/TD = fraction of time per day in large meals
NVD = number of visits per day
NMD = number of meals per day
NLX = number of large meals per day
NMD/NVD = ratio between number of meals and number of visits
NLX/NMD = fraction of large meals per day

FIV = feed intake per visit (g)
FIM = feed intake per meal (g)
FLX = FILX/NLX = feed intake per large meal (g)
RFI = FID/TD = rate of feed intake (g/min)
RFIX = FILX/TDLX = rate of feed intake in large meals (g/min)
FILX = feed intake per day in large meals (g)
FILX/FID = fraction of feed intake per day in large meals

Statistical analysis

Correlations between feed intake pattern traits and FID, production traits, pFID and RFID were estimated after correction for batch, sex and breed effects and interactions (model 3; Harvey, 1977). Pen effect was not included, because it had no significant effect on daily feed intake.

$$Y_{ijkl} = \mu + B_i + S_j + R_k + B \times S_{ij} + B \times R_{ik} + S \times R_{jk} + e_{ijkl} \qquad (3)$$

where: Y_{ijkl} = FID, RFID, pFID or production trait; μ = adjusted mean; B_i = batch effect (i=1,...5); S_j = sex effect (j=1,2); R_k = breed effect (k=1,2); BxS_{ij} = interaction effect between batch and sex; BxR_{ik} = interaction effect between batch and breed; SxR_{jk} = interaction effect between sex and breed; e_{ijkl} = error term

It was found in laying hens that feed intake activity accounted for variation in RFID (Braastad and Katle, 1989). Due to a higher level of total activity, energy requirements in the low-efficiency line were 16% higher than in the high-efficiency line. In pigs, feed intake traits recorded with the IVOG-station may describe the individual level of feed intake activity and, therefore, explain variation in RFID. To estimate the relevance of variation in feed intake activity, model (1) was extended with feed intake pattern traits: $\sum_{p=5}^{8} (b_p Z_{ijklmp})$

where: Z_{ijklmp} = covariables describing eating behaviour (p = 5,...,8).

With the directive RSELECT (Genstat 5 Reference Manual, 1987) the best model was selected with regard to Z_{ijklmp} (to a maximum of four traits) based on adjusted R^2 and mean square error.

RESULTS

Performance

The means, standard deviations and correlations are all adjusted for breed, batch, sex and interactions, according to model (3).

Least squares means, error standard deviations (SD) and coefficients of variation (CV) for number of fattening days (ND), observed daily feed intake (FID), metabolic body weight (MBW) and the various production traits are shown in Table 1. Variation coefficients ranged from 4 to 15%, with rather small variations for ND, MBW, IVO and HGP (CV: 4 to 8%).

TABLE 1. Least squares means, residual standard deviations (SD) (model 3) and coefficients of variation (CV in %) for number of fattening days (ND), observed daily feed intake (FID), metabolic body weight (MBW) and production traits: daily weight gain (WG), lean percentage in the carcass (IVO and HGP), ultrasonic backfat thickness at 170 days of age (BT), weight at start (W_0), approximated body lean (LEAN) and body fat (FAT) deposition.

Trait	Mean	SD	CV
ND (d)	114.2	6.9	6
FID (kg)	1.992	0.260	13
MBW ($kg^{0.75}$)	25.6	2.0	8
WG (g/d)	658.5	72.3	11
IVO (%)	59.0	2.2	4
HGP (%)	53.4	2.2	4
BT (mm)	11.4	1.7	15
W_0 (kg)	26.8	3.3	12
LEAN (g/d)	388.0	38.8	10
FAT (g/d)	270.5	38.1	14

The correlation coefficients between FID, MBW and production traits are shown in Table 2. Absolute values of correlation coefficients with FID were between 0.3 and 0.5 ($P<0.01$), with exception of correlations for MBW and W_0, which were 0.19 and 0.22 ($P<0.01$), respectively. MBW was strongly correlated (ca. 0.4) with WG and the - with WG strongly correlated (ca. 0.9) traits - LEAN and FAT, but absolutely weaker with the other production traits. The traits BT, IVO and HGP, which were actually measuring body composition, were mutually strongly correlated (ca. 0.65). BT had the highest correlation with WG (0.5). WG was negatively correlated with IVO and HGP lean percentages (ca. -0.4).

TABLE 2. Correlations between observed daily feed intake (FID), metabolic body weight (MBW) and production traits: daily weight gain (WG), lean percentage in the carcass (IVO and HGP), ultrasonic backfat thickness at 170 days of age (BT), weight at start (W_0) and approximated body lean (LEAN) and fat (FAT) deposition. Corrections are made for sex, breed and batch (model 3).

	FID	MBW	WG	IVO	HGP	BT	W_0	LEAN
MBW	0.19							
WG	0.47	0.44						
IVO	-0.39	-0.18	-0.41					
HGP	-0.30	-0.28	-0.39	0.65				
BT	0.35	0.25	0.50	-0.65	-0.65			
W_0	0.22	-0.01	0.23	-0.21	-0.14	0.27		
LEAN	0.37	0.42	0.94	-0.09	-0.19	0.31	0.17	
FAT	0.51	0.41	0.94	0.70	-0.55	0.64	0.26	0.77

probabilities:
$r \geq 0.14$ = $P < 0.05$
$r \geq 0.18$ = $P < 0.01$

Residual Feed Intake

Pen and sex effects and interaction effects between breed, batch and sex on FID were not significant. Therefore, these effects were left out of model (1). In addition to the fixed effects batch and breed ($P<0.05$) and the covariable MBW ($P>0.05$), the best model, selected with regard to X_{ijklmn}, contained the production covariables WG and IVO ($P<0.01$). The adjusted R^2 for this model was 0.32.

Therefore, RFID was calculated per pig with the following model:

$$RFID_{ijk} = FID_{ijk} - (\mu + B_i + R_j + 18 \times 10^{-3}\, MBW_{ijk} + 85 \times 10^{-5}\, WG_{ijk} - 28 \times 10^{-3}\, IVO_{ijk}) \qquad (4)$$

where: $RFID_{ijk}$ = residual daily feed intake (kg/d); FID_{ijk} = observed daily feed intake (kg/d); μ = adjusted mean; B_i = batch effect; R_j = breed effect; MBW_{ijk} = metabolic body weight ($kg^{0.75}$); WG_{ijk} = daily weight gain (g/d); IVO_{ijk} = IVO lean percentage

The mean RFID was zero as expected by definition. The standard deviation of RFID was 0.214 kg/d. Correlations between RFID and production traits are not significantly different from zero ($P>0.05$). Figure 1 shows the distribution of RFID. The W-test for normality (Shapiro and Wilk, 1965) resulted in significant non-normality ($P<0.05$). Skewness and kurtosis values were 0.40 and 0.11, respectively. Although these statistics give an indication for deviation from normality, further analysis have been performed without prior transformations.

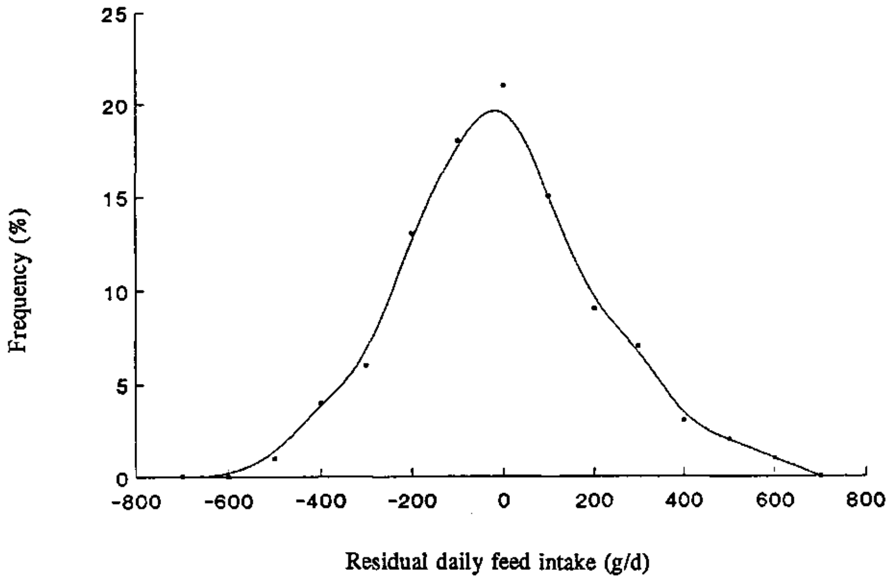

FIGURE 1. Frequency distribution of residual daily feed intake of group housed pigs.

Relations with feed intake pattern

The estimated means, standard deviations (SD) and coefficients of variation (CV) for the traits describing feed intake pattern are shown in Table 3. Pigs visited the feed hopper on average 18 times per day and spent 57 minutes per day eating. The mean of NMD/NVD was 0.67. This indicates that most visits occurred with a space of more than five minutes between them or were interrupted by another pig. On average, 62% of the number of meals per day consisted of large meals. These large meals together accounted for the major part of TD and FID (89% and 92% respectively). The rate of feed intake in large meals did not differ from the overall rate of feed intake, indicated by similar average RFI and RFIX. CV values were quite high (19% to 37%) for traits not expressed as fractions.

TABLE 3. Least squares means, residual standard deviations (SD) (model 3) and coefficients of variation (CV in %) for traits describing eating frequency, duration (min), amount (g) and rate of feed intake (g/min).

	Mean	SD	CV
time per visit (TV)	3.93	1.35	34
time per meal (TM)	5.62	1.60	29
time per large meal (TLX)	7.62	2.69	35
time per day (TD)	56.9	10.8	19
time per day in large meals (TDLX)	50.2	10.3	21
fraction of time per day in large meals (TDLX/TD)	0.89	0.07	8
number of visits per day (NVD)	18.0	5.22	29
number of meals per day (NMD)	11.7	2.77	24
number of large meals per day (NLX)	7.28	2.08	29
ratio between number of meals and number of visits (NMD/NVD)	0.67	0.09	13
fraction of large meals per day (NLX/NMD)	0.62	0.09	15
feed intake per visit (FIV)	137.1	50.3	37
feed intake per meal (FIM)	195.9	57.0	29
feed intake per large meal (FLX)	261.5	87.4	33
rate of feed intake (RFI)	34.9	5.3	15
rate of feed intake in large meals (RFIX)	34.9	5.2	15
feed intake per day in large meals (FILX)	1718.5	277.8	16
fraction of feed intake per day in large meals (FILX/FID)	0.92	0.08	9

Correlations between feed intake pattern traits and FID, production traits, pFID, RFID are shown in Table 4. For eating rate traits significant correlations occurred primarily with pFID and production traits, whereas for traits describing eating frequency and duration of daily feed intake, significant correlations occurred with FID and RFID.

TABLE 4. Correlations between feed intake pattern traits and production traits, observed daily feed intake (FID), predicted daily feed intake (pFID) and residual daily feed intake (RFID) after correction for sex, breed and batch number (model 3).

	HGP	IVO	BT	WG	pFID	RFID[#]	FID
TV	-0.16	-0.08	0.18	0.18	0.11	-0.15	-0.06
TM	-0.16	-0.11	0.17	0.19	0.16	0.00	0.09
TLX	-0.14	-0.11	0.16	0.11	0.09	0.09	0.16
TD	-0.03	-0.03	-0.05	-0.06	0.04	0.64	0.55
TDLX	-0.05	-0.03	0.01	-0.02	0.03	0.63	0.54
TDLX/TD	-0.05	0.00	0.09	0.09	0.03	0.03	0.04
NVD	0.08	0.06	-0.15	-0.14	-0.07	0.51	0.38
NMD	0.11	0.11	-0.19	-0.22	-0.14	0.45	0.29
NLX	0.09	0.09	-0.14	-0.14	-0.11	0.31	0.19
NMD/NVD	-0.01	0.04	0.03	-0.04	-0.09	-0.33	-0.32
NLX/NMD	-0.01	0.01	0.00	0.09	-0.01	-0.12	-0.10
FIV	-0.25	-0.21	0.33	0.41	0.32	-0.20	0.02
FIM	-0.29	-0.28	0.36	0.49	0.42	-0.07	0.18
FLX	-0.24	-0.25	0.32	0.34	0.33	0.06	0.24
RFI	-0.18	-0.29	0.35	0.50	0.43	-0.04	0.21
RFIX	-0.19	-0.29	0.35	0.47	0.41	-0.03	0.21
FILX	-0.26	-0.32	0.32	0.40	0.46	0.72	0.85
FILX/FID	-0.04	0.00	0.07	0.05	0.03	0.04	0.05

probabilities:
$r \geq 0.14$ = $P < 0.05$
$r \geq 0.18$ = $P < 0.01$

: RFID = FID - pFID - Fixed effects

Eating rate traits were significantly positively correlated with growth rate and backfat thickness, but significantly negatively with lean percentage. The correlations show, that pigs that eat slowly and in small meals will have a high lean percentage, but also a low daily gain. When feed intake traits and production traits were corrected for level of daily feed intake, (residual) correlations of frequency of eating and of daily eating time with lean percentage were significantly positive, correlations with daily gain and backfat thickness were significantly negative.

Correlations of feed intake pattern with production traits were reflected in correlations with pFID. pFID was positively correlated ($P<0.01$) with all eating rate traits, describing meal size and rate of feed intake, with exception of FILX/FID. This means that a high predicted feed intake will be related to a high eating rate in all meals including the large ones. There were no clear correlations of pFID, or of one of the production traits, with eating frequency and duration traits.

Correlations with FID and RFID with frequency and duration traits were very similar. FID and RFID were positively correlated with TD, NVD and NMD, negatively correlated with NMD/NVD, but not clearly correlated with TV and TM. This means that a high (residual) feed intake is related to a long total eating time, mainly caused by a large number of many consecutive visits to the feed hopper. With regard to the large meals, FID and RFID were significantly positively correlated with TDLX and NLX, not clearly correlated with TLX and not correlated with NLX/NMD and TDLX/TD. Thus in absolute terms, pigs with a high (residual) feed intake will spend much time in large meals because they have a high frequency of these meals. Proportionally however, there will be no difference in the number of large meals or in the amount of time spent in large meals between pigs, with a high or low (residual) feed intake.

With regard to the eating rate traits, FID was significantly positively correlated with RFI, RFIX, FILX and FLX and weakly with FIM, whereas RFID was positively correlated with FILX and negatively with FIV. Thus there seems to be no difference in eating rate between pigs with a high or low residual daily feed intake, whereas pigs with a high daily feed intake appear to have a high RFI.

To quantify the total influence of eating frequency and duration traits on FID and RFID, model (4) was extended with these traits. The best model, selected with regard to Z_{ijklmp}, contained the covariables TD and NVD ($P<0.01$). Covariables MBW, WG and IVO were all significant ($P<0.01$). The adjusted R^2 for this model was 0.64.

$$\begin{aligned} FID_{ijk} = {} & \mu + B_i + R_j + 42 \times 10^{-3}\, MBW_{ijk} + 70 \times 10^{-5}\, WG_{ijk} - 25 \times 10^{-3}\, IVO_{ijk} \\ & - 10 \times 10^{-3}\, TD_{ijk} + 12 \times 10^{-3}\, NVD_{ijk} + e_{ijk} \end{aligned} \tag{5}$$

where: FID_{ijk} = observed daily feed intake (kg/d); μ = adjusted mean; B_i = batch effect; R_j = breed effect; MBW_{ijk} = metabolic body weight ($kg^{0.75}$); WG_{ijk} = daily weight gain (g/d); IVO_{ijk} = IVO lean percentage; TD_{ijk} = daily eating time (min/d); NVD_{ijk} = number of visits per day; e_{ijk} = error term

DISCUSSION

Residual Feed Intake

Concluding from model (4), 32% of the variation in observed daily feed intake (FID) among individual pigs appears to be related to variation in batch, breed, metabolic body weight (MBW), daily weight gain (WG) and IVO lean percentage (IVO). This value falls within the range reported by Foster et al. (1983; 7 to 40%); he included MBW, WG and a fat index at the end of test (based on ultrasonic fat measurements) in the model. Experimental errors in measuring FID, body weight and body composition will always be part of the unexplained variation, but the high heritabilities of RFID (0.19 to 0.67) estimated by Foster et al. (1983) indicate, that a large part of it will be systematic too. A further comparison of the results of the two studies shows, that the standard deviations of FID and RFID were lower in the one by Foster et al. (1983; 5 and 6% of the average feed intake, respectively) than in the present one (13 and 11% of the average feed intake). The most important deviation from the present study is, that the pigs of Foster et al. (1983) were housed individually and fed to appetite during a short period of the day to get individual feed intake data. Corresponding figures about individual feed intake measurements of group housed pigs, like in the present experiment, could not be found in literature.

Another reason for the rather low R^2 will be that the variances of MBW and IVO were quite small in the present experiment (Table 1). This may be caused partly by the choice of the test period (starting and ending at, more or less, fixed body weights per pen) and partly by the way of assigning pigs to pens (only boars or only gilts and with almost similar body weights). Starting and ending at fixed body weights per pig, in the individual housing experiment of Foster et al. (1983), will be the main cause of his even smaller coefficients of variation for MBW (2 to 3%).

As a consequence of the small variation by the fixed weight interval, the effect of choosing any power (like e.g. 0.75) for MBW will have a negligible effect on the amount of variation explained by the model, especially in combination with inclusion of an intercept in the model (Noblet et al., 1988; Luiting and Urff, 1991). Furthermore, by using the average MBW during the test period, metabolic body weight gain, expressed as changes in metabolic body weight during test, was assumed to be linear. During the third batch pigs were weighed every two weeks; there was no significant difference between MBW based on these two-week weighings and MBW based on start and end weighings only, and a correlation of 0.96 between the two alternatives was found. Thus the assumption of a linear metabolic body weight gain seems to be acceptable with regard to MBW in the present experiment.

The R^2 value of 0.32 is somewhat lower, but comparable to literature concerning growing animals of various other species (34 to 52% in beef cattle (Koch et al., 1963); 38% in growing heifers in dairy cattle (Korver et al., 1991); 22 to 77% in growing cocks of a laying strain (Luiting, 1991). In these studies, no measurement for body composition was used. Especially the standard deviations of RFID (error standard deviations of model) were lower in these reports (3 to 8% of the average feed intake) than in the present study (11% of the average feed intake). Again, animals were individually housed and/or individually fed to appetite like in the experiment of Foster et al. (1983). Corresponding figures about individual feed intake measurements in group housed animals are lacking in literature. Moreover, in the reports mentioned, concerning the other species, experiments were conducted over a fixed time interval, thus allowing more variation in MBW and body composition.

In conclusion, for group housed pigs measured over the same weight interval, a small fraction of the variation in individual FID appears to be explained by MBW, WG and IVO, in relation to literature concerning individually housed animals and fixed time intervals.

Energy requirements have been calculated by estimating the maintenance part (related to weight) and the production part, estimated from its relation to live weight gain and to IVO lean percentage as a value for body composition.

In model (4) the regression coefficient for MBW was not significant. This was undoubtedly due to the low coefficient of variation for MBW, together with a strong correlation of WG with daily feed intake and with MBW. In model (5) regression coefficients for all covariables were significant, due to lower standard errors. The maintenance requirements per metabolic kilogram, derived from the partial regression coefficient for MBW in model (4) and adjusted for mean FID, were 795 ± 204 kJ ME/kg$^{0.75}$ (ME content of the feed was estimated from the calculated Net Energy content as 9.1/0.7 = 13 MJ/kg). In model (5), after correction for feed intake traits, maintenance requirements per kg metabolic body weight were lower: 634 kJ ME/kg$^{0.75}$. These estimations were at the upper boundary of the range given by the NRC (1988) of 371 to 646 kJ ME/kg$^{0.75}$ d. The small variation in body weight caused a relatively high sampling error on the partial regression coefficient for MBW. In a sample of the presented data De Haer and De Vries (1992) found a low digestibility of the feed in comparison with the literature. Thus, the true ME content of the feed will probably be lower in the present experiment. Furthermore, the values given by the NRC (1988) are mainly based on feeding trials with different energy levels and calorimetric trials with often individually housed pigs under strongly controlled experimental conditions (ambient temperature, feeding scheme, housing, etc.). Maintenance requirements in the present experiment may be absolutely higher by the higher activity level in group housed pigs. In the literature the effects of the other factors on activity are not so clear by lack of information on activity. In poultry

Grimbergen (1974) reported a similar discrepancy in maintenance requirements between estimates based on multiple regressions under practical conditions and estimates based on calorimetry. He concluded that the large differences in environmental conditions between these two kinds of investigations are the main reason for it.

Energy requirements for production have been related to WG and IVO. The amount of feed needed for a daily body weight gain equal to the average WG (658.5 g/d) with the average IVO lean percentage (59%), was calculated as 0.65 kg/d. To calculate this amount of feed, the partial regression coefficient in model (5) for WG was also used. 0.65 kg/d Is below the range of values (0.90 to 1.62), calculated by using the range of energy requirements for protein and fat given by the NRC (1988; assuming 20% of protein in lean tissue and 13 MJ ME/kg feed). The underestimation of the energy requirements for daily gain together with the above-mentioned overestimation of the energy requirements for maintenance compared to the NRC (1988) values, is often found in literature about growing animals (Van Es, 1982; Korver et al, 1991). However, it is difficult to draw conclusions on estimated regression coefficients if they are highly correlated (Van Es, 1982), which is especially the case for MBW and WG (-0.81). The changes in feed associated with MBW and WG by adding activity traits to the model, depend on the sizes of the correlations. Therefore, the interpretation of the changes in these partial regression coefficients from model (4) to model (5), caused by adding the activity traits, is disputable too.

The differences in R^2 between the models with either IVO, HGP or BT were very small. IVO seems to give the best results, followed by HGP and then BT. This order is the same as expected from their correlations with meat percentage, measured by the EC-reference method (0.97, 0.87 and -0.72, respectively; Walstra, 1987). Respective correlations with chemically determined body protein were lower (De Greef, personal communication, 1991). This means that by using IVO as indication for the real lean percentage, a part of at least 6% of the total variation in daily feed intake is not explained. Furthermore, IVO is an indication of carcass composition only at end of a test. In relation to a growth model in pigs, Moughan and Verstegen (1988) concluded that protein content of the body at start of test was quite constant, but that fat content may vary quite considerably between individuals. However, they found in the literature that fat content was highly correlated with body weight at start of test, and that it had no effect on growth performance to 60 kg. According to this, body weight at start of test (W_0) was included in the model in the present report (having no information of fat content measurements at start of test), but it did not increase adjusted R^2.

Fat and lean tissue gain may not be linear during test. A better estimation of the variation in fat and lean deposition (and therefore also of the variation in corresponding maintenance requirements) will be obtained when body composition is measured regularly within animals. This could be done, for example, by utilising computerised tomography (CT) (Vangen, 1988) or NMR spectroscopy (Mitchell et al, 1991). This means that in our data variation in fat and lean deposition during test does not explain all variation in FID. Some variation in body composition has not been measured or included by our way of measuring lean and fat. In laying hens variations in egg and body composition seem to be of minor importance with regard to the unexplained variation in FID, whereas the largest part of this RFID variation was related to variation among animals in maintenance requirements per unit metabolic body weight (other than the part related to body composition), and especially to variation in activity and thermoregulation (Luiting, 1991).

Relations with feed intake pattern

Digestibility and availability of amino acids

Relationships between lean tissue formation and meal size may exist through relations of digestibility and availability of nutrients with the distribution of feed intake during the day. In rats nitrogen retention was positively correlated with feeding frequency at equal levels of daily feed intake (Fábry, 1967). For individually housed pigs, Friend and Cunningham (1964) reported no significant effect on carcass composition by feeding pigs once or five times daily with the same total amount of feed. Frequency of eating in pigs may have less influence on fat and lean formation than in rats, because they are expected to have a lower rate of passage through the intestinal tract (O'Hea and Leveille, 1969). This means a more continuous supply of nutrients in pigs compared to rats.

However, there are some indications that at a high eating frequency the availability of essential amino acids may be positively influenced, because amino acids can rapidly disappear from the body when they are not utilised (Batterham and Bayley, 1989; Den Hartog et al., 1989). Cohn et al. (1962) showed that, at a low feeding frequency urinary nitrogen excretion was increased.

Eating frequency was also positively related with digestibility of the feed (Van Kempen et al., 1979; De Haer and De Vries, 1992). This may be related to rate of passage (Ruckebusch and Bueno, 1976; Sissons and Jones, 1991) and to digestive enzyme production (Hee et al., 1988; Xu et al., 1991).

In the present study, there were no clear correlations (Table 4) between production traits and eating frequency and duration, but meal size and rate of feed intake were clearly associated with performance. Pigs with a low rate of feed intake and small meals had a high lean percentage. When level of daily feed intake was corrected for, frequency of eating was positively related with lean percentage. It can be concluded that meal size, and frequency of eating when daily feed intake is equal among pigs, are negatively, respectively positively, related with lean percentage through a better digestibility of feed and a better availability of amino acids throughout the day.

However, pigs with a low rate of feed intake and small meals had a low pFID and a low daily weight gain. Relationships between meal frequency and daily gain are reported in studies, examining relationships between ranking order and performance in group housing. Higher ranking pigs had a higher daily gain (Jonsson, 1985; Peters, 1989) and less but larger meals (Peters, 1989). In the present study, positive relations were found between meal size and daily gain, whereas frequency of eating was negatively related with daily gain. The latter relationship was more negative when daily gain and frequency of eating were corrected for level of daily feed intake. This relation can be explained, because frequency of eating is also related to level of activity.

Activity

Feed intake traits were analysed to study the relation between feed intake activity and RFID. Correlations of eating frequency and daily eating time with RFID were highly significant. Correlations of eating frequency and duration traits with FID and RFID were quite similar. Correlations of RFID and FID were almost zero with regard to eating rate.

A low RFID means a more efficient pig, that requires less feed than the average pig for a certain level of metabolic body weight and production. Pigs with a low RFID had less visits and meals and spent, therefore, less time eating per day than pigs with a high RFID. Furthermore, NMD/NVD was higher, indicating that the visits were more spread out over the whole day. To quantify the total influence of eating frequency and duration ('feed intake activity') traits on RFID, model (4) was extended with these traits; the adjusted R^2 increased from 0.32 to 0.64. This means that variation in the amount of feed intake activity accounted for 47% (i.e. (0.64-0.32)/(1-0.32)) of the variation in RFID. This figure agrees well with estimates for (feed intake) activity in laying hens in the literature (Braastad and Katle, 1989; Luiting et al. (1991)). Measuring feed intake pattern as in the present experiment (i.e. only the time and frequency of meals) will probably underestimate total feed intake activity. Together with the fact that other forms of activity may cost feed too, this means that the part of RFID which is related to total activity will even be higher.

Implications

Recapitulating, variation in daily feed intake between pigs was for 32% related to a linear combination of metabolic body weight, daily weight gain and lean percentage. The R^2 indicates that a large part of the variation in FID consists of RFID. Traits of feed intake pattern were clearly associated with RFID. It can be concluded, that a high RFID coincides with a long daily eating time and a high eating frequency. A combination of a high production level with a low RFID will result in an efficient pig. Therefore, a pig should have a high 'appetite for production', but a low 'appetite for RFID'. It is derived that this may lead to an animal with a short daily eating time, a low eating frequency and large meal sizes.

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REFERENCES

Bergström, P.L. and Kroeske, D., 1968. Methods of carcass assessment in research on carcass quality in the Netherlands. I. Description of the methods. EAAP meeting Dublin; IVO-report C-123, Zeist, The Netherlands.

Braastad, B.O. and Katle, J., 1989. Behavioral differences between laying hen populations selected for high and low efficiency of food utilization. Br. Poultry Sci., 30:533-544.

Cohn, C., Joseph, D. and Allweiss, M.D., 1962. Nutritional effects of feeding frequency. Am. J. Clinic. Nutr., 11:356-361.

De Haer, L.C.M. and Merks, J.W.M., 1992. Patterns of daily feed intake in growing pigs. Anim. Prod., 54 (in press).

De Haer, L.C.M., Merks, J.W.M., Kooper, H.G. and Van Hattum, J.A., 1992. A note on the IVOG®-station: a feeding station to record the individual feed intake of group housed growing pigs. Anim. Prod., 54 (in press).

De Haer, L.C.M. and De Vries, A.G., 1992. Feed intake patterns and feed digestibility of growing pigs housed individually or in groups. Livest. Prod. Sci. (accepted).

Den Hartog, L.A., Verstegen, M.W.A. and Huisman, J., 1989. Amino acid digestibility in pigs as affected by diet composition. In: Friedman, M. (Editor), Absorption and utilization of amino acids, Vol. III., CRC Press, Florida, pp. 201-216.

Fábry, P., 1967. Metabolic consequences of the pattern of feed intake. In: Code, F.P. (Editor), Handbook of physiology, Sect. 6: Alimentary canal. Am. Physiol. Soc., pp. 31-49.

Foster, W.H., Kilpatrick, D.J. and Heaney, I.H., 1983. Genetic variation in the efficiency of energy utilization by the fattening pig. Anim. Prod., 37:387-393.

Friend, D.W. and Cunningham, H.M., 1964. Effects of feeding frequency on metabolism, rate and efficiency of gain and on carcass quality of pigs. J. Nutr., 83:251-256.

Genstat 5 Committee, 1987. Genstat 5 Reference Manual. Oxford University Press, Great Britain.

Grimbergen, A.H.M., 1974. Energy expenditure under productive conditions. In: Morris, T.R. and Freeman, B.M. (Editors), Energy requirements of poultry, Br. Poultry Sci., Edinburgh, Scotland, pp. 61-71.

Halter, H.M., Wenk, C. and Schürch, A., 1979. Effect of feeding level and feed composition on energy utilization, physical activity and growth performance of piglets. In: Mount, L.E. (Editor), Proc. Eight Symposium on Energy Metabolism, Cambridge, United Kingdom. EAAP publ. no. 26, Butterworths, London, pp. 395-398.

Harvey, W.R., 1977. User's guide for LSML76 (Mixed Model Least Squares and Maximum Likelihood Computer Program). Mimeo, Ohio State University, 76 pages.

Hee, J., Sauer, W.C. and Mosenthin, R., 1988. The effect of feeding on the pancreatic secretions in the pig. J. Anim. Physiol Nutr., 60:249-256.

Jonsson, P., 1985. Gene action and maternal effects on social ranking and its relationship with production traits in pigs. Z. Tierzücht. Züchtgsbiol., 102:208-220.

Koch, R.M., Swiger, L.A., Chambers, D. and Gregory, K.E., 1963. Efficiency of feed use in beef cattle. J. Anim. Sci., 22:486-494.

Korver, S., Van Eekelen, E.A.M., Vos, H., Nieuwhof, G.J. and Van Arendonk, J.A.M., 1991. Genetic parameters for feed intake and feed efficiency in growing dairy heifers. Livest. Prod. Sci., 29:49-59.

Luiting, P. and Urff, E.M., 1987. Residual feed intake: a new source of genetic variation for feed efficiency. 38th. Annual Meeting of the European Association for Animal Production, Lisbon, Portugal, GNC4.8: 6 pp.

Luiting, P., 1991. The value of feed consumption data for breeding in laying hens. PhD thesis Wageningen Agricultural University, The Netherlands, pp. 115-137.

Luiting, P. and Urff, E.M., 1991. Optimisation of a model to estimate residual feed consumption in the laying hen. Livest. Prod. Sci., 27:321-338.

Luiting, P., Schrama, J.W., Van der Hel, W. and Urff, E.M., 1991. Metabolic differences between White Leghorns selected for high and low residual feed consumption. Br. Poultry Sci., 32:763-782.

Metz, S.H.M., Bergström, P.L., Lenis, N.P., De Wijs, M. and Dekker, R.A., 1980. The effect of daily energy intake on growth rate and composition of weight gain in pigs. Livest. Prod. Sci., 7:79-87.

Mitchell, A.D., Wang, P.C., Elsasser, T.H. and Schmidt, W.F., 1991. Application of NMR spectroscopy and imaging for body composition analysis as related to sequential measurement of energy deposition. Proc. 12th Symposium on Energy Metabolism in Farm Animals, Kartause Ittingen, Switzerland, 4 pp.

Moughan, P.J. and Verstegen, M.W.A., 1988. The modelling of growth in the pig. Neth. J. Agric. Sci., 36:145-166.

Noblet, J., Karege, C. and Dubois, S., 1988. Influence of sex and genotype on energy utilisation in growing pigs. In: Van der Honing, Y. and Close, W.H. (Editors), Proc. 11th Symposium on Energy Metabolism in Farm Animals, Lunteren, The Netherlands. EAAP publ. no. 43, pp. 57-60.

NRC, 1988. Nutrient requirements of swine. 9th Revised edition, National Research Council. National Academy Press, Washington, D.C., U.S.A., 93 pp.

O'Hea, E.K. and Leveille, G.A., 1969. Influence of feeding frequency on lipogenesis and enzymatic activity of adipose tissue and on the performance of pigs. J. Anim. Sci., 28:336-341.

Peters, B., 1989. Verhaltensbeobachtungen an Mastschweinen während der fresszeit bei zeitlich begrenzter Mahlzeitenfütterung. Tierzucht, 43:590-592.

Ruckebusch, Y. and Bueno, L., 1976. The effect of feeding on the motility of the stomach and small intestine in the pig. Br. J. Nutr., 35:379-405.

Shapiro, S.S. and Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika, 52:591-611.

Sissons, J.W. and Jones, C.L., 1991. Ultrasonic and electromyographic measurements of the effects of feed intake on digesta flow and gastro-intestinal motility in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no. 54, Pudoc, Wageningen, The Netherlands, pp. 120-125.

Van Es, A.J.H., 1982. Energy metabolism in pigs. A review. In: Ekern, A. and Sundstøl, F. (Editors), Proc. 9th Symposium on Energy Metabolism in Farm Animals, Lillehammer, Norway. EAAP publ. no. 29, pp. 249-255.

Vangen, O., 1988. Experience from several years of using of computerised tomography (CT) in animal breeding research. 6th World Conference on Animal Production, Helsinki, Finland, paper 437.

Vangen, O. and Kolstad, N., 1986. Genetic control of growth, composition, appetite and feed utilization in pigs and poultry. 3th World Conference on Genetics Applied to Livestock Production, Nebraska, U.S.A., Vol. XI:367-380.

Van Kempen, G.J.M., Boer, H., Van der Poel, A.F.B. and Van Poppel, F.J.J., 1979. Effect of frequency of feeding and dietary treatment on metabolism, performance and carcass characteristics of swine. Neth. J. Agric. sci., 27:199-210.

Verstegen, M.W.A., Van der Hel, W., Brandsma, H.A. and Kanis, E., 1982. Heat production of groups of growing pigs as affected by weight and feeding level. In: Ekern, A. and Sundstol, F. (Editors), Proc. 9th Symposium on Energy Metabolism in Farm Animals, Lillehammer, Norway. EAAP publ. no. 29, pp. 218-221.

Walstra, P., 1987. The instrumental classification and grading of pigs in the Netherlands. Workshop "Experiences in Europe about pork objective grading", Reggio Emilia, Italy.

Xu, R.-J., Cranwell, P.D. and Hennessy, D.P., 1991. Effects of method of feeding and meal size on the postprandial gastrin response in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no. 54, Pudoc, Wageningen, The Netherlands, pp. 41-46.

Chapter 5

GENETIC ASPECTS OF THE FEED INTAKE PATTERN OF GROUP HOUSED GROWING PIGS

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ABSTRACT

During five batches individual feed intake patterns were recorded of 273 group housed Dutch Landrace (DL) and 132 group housed Great Yorkshire (GY) pigs. In each group pen 8 pigs were housed, of one sex and breed. Feed intake was ad libitum. Pigs were tested from 25 to 35 kg at the beginning until an average live weight per pen of 100 kg was reached. From each pig growth rate (WG), ultrasonic backfat thickness (BT), feed conversion (FC) and lean percentage (IVO, HGP) were measured.

Production traits and feed intake pattern were significantly influenced by breed ($P<0.01$ and $P<0.05$, respectively), with exception of daily feed intake ($P>0.05$). GY pigs had a better WG, FC, IVO and HGP than DL pigs. GY ate more frequently, in smaller meals and less daily eating time compared with DL, at almost equal FID. It was suggested that GY pigs had a higher maximum rate of protein deposition and lower maintenance requirements per kg metabolic body weight. These factors may explain the high lean deposition and low fat deposition in GY pigs. Boars had significantly higher growth rate and better feed conversion ($P<0.01$) than gilts. Feed intake per visit was significantly higher for boars, whereas frequency of eating was lower ($P<0.05$).

Heritability estimates for feed intake traits were low to moderate. It is concluded that the feed intake pattern is genetically determined, although standard errors were considerable. Number of visits and meals per day and feed intake per visit and per meal had moderate heritabilities.

INTRODUCTION

In animals, composition of gain is regulated by physiological mechanisms, influencing daily feed intake, meal size and frequency and energy dissipation (activity, thermogenesis). The physiological mechanisms can be genetically determined (Owen, 1990). Genotypic effects on body composition may involve factors as: potential maximum protein deposition (Campbell et al., 1985; Campbell and Taverner, 1988; Metz et al., 1980), maintenance requirements per kg metabolic weight (Campbell et al, 1985; Campbell and Taverner, 1988; Sundstøl et al., 1979; Henken et al., 1991) and partial efficiencies for utilisation of energy for components of body weight gain (Metz et al., 1980; Sundstøl et al., 1979).

Campbell et al. (1985) and Metz et al. (1980) indicated that there is an effect of sex on growth performance. They reported a higher potential maximum protein deposition and higher energy requirements for maximum protein deposition for boars compared to gilts. This means, that a decrease in protein deposition, due to a restriction in energy intake, may be greater for boars than for gilts. Boars will have a higher daily protein gain, but total energy retained may be higher for gilts, having lower maintenance requirements per kg metabolic body weight (Campbell et al., 1985).

Lean breeds may have a higher potential maximum protein deposition and/or a higher age of maturation (Henken et al., 1991; Krieter and Kalm, 1989; Sundstøl et al., 1979). Because of a greater mass of 'active' tissue, maintenance requirements per kg metabolic weight will be higher for lean breeds (Sundstøl et al., 1979). On the other hand, Henken et al. (1991) reported higher maintenance requirements per metabolic kg for the fat and slower growing lines, because of a higher level of activity. This indicates, that for maintenance requirements the level of activity may be more important than lean percentage.

It has previously been shown that feed intake pattern influences efficiency of production, digestion and utilisation of nutrients for fat and lean deposition (De Haer and De Vries, 1992; De Haer et al., 1992a). Residual feed requirements after accounting for metabolic body weight, lean percentage and daily weight gain, are termed residual daily feed intake (RFID) (Luiting, 1991). A high RFID indicates a non-efficient pig. For group housed pigs significant correlations were found between feed intake pattern, production traits and RFID (De Haer et al., 1992a). Feeding frequency and daily eating time were significantly positively correlated with RFID; meal size and rate of feed intake were significantly correlated with production traits. Feed intake pattern, especially frequency of eating and meal size, has been reported to be related to the availability of essential amino acids (Batterham and Bayley, 1989; Den Hartog et al., 1989), and with digestibility (De Haer and De Vries, 1992; Van Kempen et al., 1979). These results indicate, that an increased daily eating time and increased frequency of eating will reduce efficiency of pigs, but improve lean percentage.

The aim of this study is, to investigate genetic aspects of feed intake pattern. Differences between breeds and sexes are studied and heritabilities of feed intake pattern traits are estimated.

MATERIAL AND METHODS

Experimental design

From September 1988 till May 1991 feed intake patterns were recorded of group housed Dutch Landrace (DL) and Great Yorkshire (GY) pigs. During the first three batches 80 DL pigs were housed in 10 pens of 8 animals per pen, the following two batches DL and GY pigs were housed in 14 group pens for 8 pigs.

The pigs were fed ad libitum. To record individual feed intake, each pen was equipped with and IVOG-station (De Haer et al., 1992b). The feeding station consisted of a feed hopper which was weighed continuously. At each visit of a pig to the feeder, time and weight of feed at the beginning and at the end of the visit were recorded automatically, together with the animal identification number. Competition for the feed was possible, as a pig was mainly unprotected during eating. Feed supplied during the first weeks of test (on average 50 kg per pig in total) contained 9.4 MJ Net Energy/kg and 182 g/kg crude protein. After this, the feed supplied for growing pigs contained 9.1 MJ Net Energy/kg and 168 g/kg crude protein.

The test started at a live weight between 25 and 35 kg. To reduce variation in final weights, pigs were grouped together according to weight. Each pen consisted of boars or gilts only. DL and GY pigs were each housed in separate pens. Litter-mates were preferably kept in separate pens too. The test was finished when the average live weight per pen was at least 100 kg, determined by weighing once a week. During test, at the age of 170 ± 10 days backfat thickness was measured ultrasonically (BT). At the end of the test live weight and meat percentage (IVO standard dissection method; Bergström and Kroeske (1968) and Hennessy Grading Probe HGP; Walstra (1987)) were determined. Daily weight gain during test (WG) and feed conversion (feed to gain ratio) (FC) were calculated.

Feed intake pattern

From the data collected with the IVOG-station the following feed intake traits describing daily frequency, duration and rate of eating could be derived (De Haer and Merks, 1992):

TV = time per visit (min)
TM = time per meal (min)
TD = time per day (min)
TDLX = time per day in large meals (min)
NVD = number of visits per day
NMD = number of meals per day
NLX = number of large meals per day
NMD/NVD = ratio between number of meals and number of visits
NLX/NMD = fraction of large meals per day
FIV = feed intake per visit (g)
FIM = feed intake per meal (g)
RFI = FID/TD = rate of feed intake (g/min)
FID = feed intake per day (g)
FILX = feed intake per day in large meals (g)

To group visits into meals, a meal criterion of 5 minutes was used according to De Haer and Merks (1992). This means that two successive visits of a pig, the second starting within 5 minutes after the first and without a visit of another pig interrupting, were added together and considered as one meal. The Linda-index (De Haer and Merks, 1992) was used to select the large meals per day that have together a major contribution to the daily feed intake.

Statistical analysis

With Least Squares analysis (Harvey, 1977) differences between breeds and sexes in feed intake pattern and production traits were analysed (model 1). Least Squares analysis was used, because fixed effects estimated with the univariate REML programme of Meyer (1989) can not be tested for significance. Litter effects were not included in model 1, for it was computational not feasible to correct for these effects.

$$Y_{ijkl} = \mu + B_i + S_j + R_k + B \times S_{ij} + B \times R_{ik} + S \times R_{jk} + e_{ijkl} \tag{1}$$

where: Y_{ijkl} = feed intake trait or production trait; μ = adjusted mean; B_i = batch effect (i=1,...5); S_j = sex effect (j=1,2); R_k = breed effect (k=1,2); BxS_{ij} = interaction effect between batch and sex; BxR_{ik} = interaction effect between batch and breed; SxR_{jk} = interaction effect between sex and breed; e_{ijkl} = error term

Residual daily feed intake (RFID) was calculated from recorded individual daily feed intake, corrected for significant fixed effects, average metabolic body weight during test, daily weight gain and IVO lean percentage at the end of test (De Haer et al., 1992a). RFID is a measure of efficiency of production. As RFID was corrected for fixed effects, sex and breed effects were zero by definition. To investigate the genetic determination of RFID, the heritability of RFID was estimated.

Data were analysed according to model (2) with the univariate REML programme of Meyer (1989) to estimate heritabilities for feed intake pattern and production traits. Variance components were estimated iteratively. The simplex procedure to minimise the log likelihood was stopped, when a convergence criterion of 10^{-5} was reached. Litter effect was included, to obtain heritability estimates corrected for common environmental effect.

$$Y_{ijklm} = \mu + B_i + S_j + R_k + B \times S_{ij} + B \times R_{ik} + S \times R_{jk} + L_{l:ik} + A_{m:ijkl} + e_{ijklm} \tag{2}$$

where in addition to model 1: Y_{ijklm} = feed intake trait or production trait; $L_{l:ik}$ = (random) litter effect within i-th batch and k-th breed; $A_{m:ijkl}$ = (random) genetic animal effect; e_{ijklm} = error term

Model (2) and mixed model equations can be expressed as follows:

$$Y = Xh + Wl + Za + e \tag{3}$$

where: X = design matrix for fixed effects; h = vector of fixed effects; W = design matrix for (random) litter effects; l = vector of litter effects; Z = design matrix for (random) animal effects; a = vector of (random) genetic animal effects = breeding value of animal; e = vector of residual errors

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}W & X'R^{-1}Z \\ W'R^{-1}X & W'R^{-1}W+\lambda_1 I & W'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}W & Z'R^{-1}Z+\lambda_2 A^{-1} \end{bmatrix} \begin{bmatrix} \bar{h} \\ \bar{l} \\ \bar{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}Y \\ W'R^{-1}Y \\ Z'R^{-1}Y \end{bmatrix}$$

where: A = numerator relationship matrix; R = matrix of residual (co-)variances V(e); I = identity matrix; $\lambda_1 = \sigma^2_e / \sigma^2_l$; $\lambda_2 = \sigma^2_e / \sigma^2_a$

RESULTS

Breed and sex effects

In Table 1 a description of production traits of DL and GY pigs is given. Batch x sex interaction and batch x breed interaction were not significant ($P>0.05$). Sex x breed interaction was significant for HGP ($P<0.05$) and IVO ($P<0.01$) lean percentage and ultrasonic backfat thickness ($P<0.05$). DL boars were leaner than DL gilts, but for GY sex differences were opposite. This effect may be caused by the higher start weight of GY boars compared to GY gilts. DL pigs had a significantly ($P<0.01$) lower growth rate, a higher feed to gain ratio, more backfat and a lower lean percentage compared to GY pigs. Boars had a significantly ($P<0.01$) better growth rate and lower feed conversion compared to gilts.

TABLE 1. Least squares means and error standard deviations (model 1) of production traits of DL and GY boars and gilts. Significances of breed (R) and sex (S) effects and of sex x breed interaction (SxR) are shown.

Trait	DL		GY		error	significance		
	boars	gilts	boars	gilts	st.d.	R	S	SxR
Growth rate (WG) (g/d)	662.9	607.8	712.8	650.7	72.3	**	**	
Feed conversion (FC)	2.98	3.21	2.59	2.95	0.37	**	**	
Backfat thickness (BT) (mm)	11.9	12.2	11.2	10.1	1.66	**		*
IVO lean percentage (IVO)	58.7	57.2	59.8	60.4	2.20	**		**
HGP lean percentage (HGP)	52.6	51.8	54.0	55.2	2.22	**		*
Weight at start (kg)	27.1	27.1	28.2	25.0	3.31		**	*
Weight at end (kg)	102.7	100.7	105.1	98.6	8.73			

probabilities:
* = $P < 0.05$
** = $P < 0.01$

Feed intake pattern (Table 2) was significantly influenced by breed and sex. No significant interactions were found. GY pigs ate more frequently and faster than DL pigs: the number of visits and number of meals per day were significantly higher, feed intake in visits and meals was less, rate of feed intake was higher and daily eating time was lower ($P<0.01$). The proportion of meals per visit (NMD/NVD) and proportion of large meals (NLX/NMD) are traits describing the distribution of feed intake over the day. A small NMD/NVD indicates, that many visits are clustered into one meal. A small NLX/NMD indicates, that a relatively small amount of meals makes a major contribution to daily feed intake, or that daily feed intake is concentrated in a few meals. GY pigs had proportionately more visits per meal ($P<0.05$) and more large meals ($P<0.01$) than DL. This indicates, that meals of GY pigs consist of many visits and that daily intake of feed was distributed over many, relatively large, meals. Daily feed intake of DL pigs was concentrated in a few large meals and many small meals, consisting of a few visits per meal. Daily feed intake was not significantly different between GY and DL pigs.

Sex effect was significant ($P<0.05$) for feed intake per visit and number of visits and meals per day. Boars ate less frequently per day, but they had a higher feed intake per visit compared to gilts.

TABLE 2. Least squares means and error standard deviations (model 1) of feed intake pattern traits of DL and GY boars and gilts. Significances of breed and sex effects are shown.

Trait	DL		GY		error	significance	
	boars	gilts	boars	gilts	st.d.	breed	sex
Time per visit (TV) (min)	4.88	4.56	3.31	2.96	1.35	**	
Time per meal (TM) (min)	6.72	6.38	4.85	4.54	1.60	**	
Time per day (TD) (min)	62.1	59.5	51.6	54.2	10.8	**	
Time per day in large meals (TDLX) (min)	54.8	52.4	45.6	48.0	10.3	**	
Number of visits per day (NVD)	15.4	15.9	18.8	21.7	5.2	**	*
Number of meals per day (NMD)	10.4	10.5	12.3	13.7	2.8	**	*
Number of large meals per day (NLX)	6.2	6.0	8.0	8.8	2.1	**	
Ratio between number of meals and number of visits (NMD/NVD)	0.69	0.68	0.66	0.64	0.09	*	
Fraction of large meals per day (NLX/NMD)	0.60	0.58	0.66	0.64	0.09	**	
Feed intake per visit (FIV) (g)	154.8	150.6	133.6	109.3	50.3	**	*
Feed intake per meal (FIM) (g)	212.8	210.1	192.8	167.9	57.0	**	
Rate of feed intake (RFI) (g/min)	33.2	31.5	37.9	36.9	5.3	**	
Feed intake per day (FID) (g)	1868	1879	1854	1862	248		
Feed intake per day in large meals (FILX) (g)	1709	1727	1713	1725	278		

probabilities:

* = $P < 0.05$

** = $P < 0.01$

Heritabilities

Heritabilities (Table 3) for production traits were relatively high, with values between 0.45 and 0.63, but standard errors were also high (around 0.22). Residual feed intake showed a high heritability of 0.45, with a low c^2 of 0.02. For the other production traits common environmental effects of 0.00 to 0.09 were found.

Heritabilities for feed intake traits, estimated according to model 3, ranged between 0.04 and 0.49, with standard errors of 0.13 to 0.24. Traits describing frequency of eating (NVD, NMD and NLX) and meal size (FIV and FIM) had moderate heritabilities of 0.35 to 0.49, whereas FILX and TDLX were hardly heritable. A high c^2 was estimated for daily feed intake, rate of feed intake and daily eating time. For these traits c^2 varied from 0.14 to 0.21.

TABLE 3. Heritabilities (h^2) and common environmental effects (c^2) of production traits and feed intake pattern, with standard error between brackets. Estimates were performed according to model 3.

	h^2	c^2
Growth rate	0.49 (0.22)	0.00 (0.10)
Feed conversion	0.51 (0.22)	0.02 (0.07)
Backfat thickness	0.57 (0.17)	0.07 (0.07)
IVO lean percentage	0.55 (0.22)	0.09 (0.10)
HGP lean percentage	0.63 (0.22)	0.01 (0.10)
Residual daily feed intake	0.45 (0.22)	0.02 (0.11)
Time per visit	0.27 (0.16)	0.00 (0.08)
Time per meal	0.27 (0.17)	0.00 (0.09)
Time per day	0.24 (0.20)	0.14 (0.09)
Time per day in large meals	0.05 (0.18)	0.18 (0.09)
Number of visits per day	0.38 (0.20)	0.04 (0.08)
Number of meals per day	0.45 (0.20)	0.00 (0.10)
Number of large meals per day	0.49 (0.22)	0.00 (0.12)
Feed intake per visit	0.35 (0.21)	0.01 (0.10)
Feed intake per meal	0.47 (0.22)	0.00 (0.10)
Rate of feed intake	0.29 (0.24)	0.21 (0.11)
Daily feed intake	0.16 (0.16)	0.14 (0.08)
Feed intake per day in large meals	0.04 (0.13)	0.04 (0.07)

DISCUSSION

Effects of breed and sex

The present results show a significant breed effect on production traits and feed intake pattern. The higher growth rate, less backfat and higher lean percentage at equal levels of daily feed intake for GY pigs compared with DL pigs suggest that the rate of muscle growth for GY is higher due to a higher upper-limit for body protein retention. A higher protein deposition in GY will decrease the available energy for fat deposition. As a result lean percentage and daily gain are higher for GY compared with DL pigs and feed conversion will be lower. Comparable results about breed differences are reported by Campbell and Taverner (1988), Henken et al. (1991) and Sundstøl et al. (1979). Henken et al. (1991) concluded, that GY pigs have a higher potential for protein gain. Moreover, they showed a higher amount of metabolisable energy available for production, because GY had a low level of activity associated heat production compared to Landrace pigs.

Sex effects were significant for daily weight gain and feed conversion, with better results for boars than for gilts. This agrees with Metz et al. (1980), who indicated that boars have a higher maximum protein deposition than gilts. As energy input was not restricted, males had a higher lean tissue gain and better feed conversion. This is comparable with results obtained by Campbell et al. (1985).

Comparison of breeds for the feed intake pattern showed a high number of visits and meals per day with less feed intake per meal for GY compared to DL pigs. However, rate of feed intake was higher and total eating time per day was lower for GY. The small meal size and high frequency of meals can have a positive effect on protein utilisation and on lean tissue formation (Batterham and Bayley, 1989; Den Hartog et al., 1989). Due to the high potential for protein gain in GY pigs, the positive influence of meal frequency on protein utilisation will have a positive effect on growth rate.

It was expected that a high frequency of eating may have a negative effect on efficiency of production, because of a high level of activity (De Haer and De Vries, 1992; De Haer et al., 1992a). However, Henken et al. (1991) reported lower maintenance requirements per kg metabolic weight for GY than for Landrace pigs, when fed restricted. This effect was due to an overall low activity level of GY, measured during the whole day and not only during eating. The low daily eating time and proportionately many large meals for GY pigs in the present study may both be an indication for this low activity level, but the high eating frequency is in disagreement with little activity. The lower maintenance requirements for GY (3.8%; Henken et al., 1991) will result in a higher amount of available metabolisable energy, to enable a high lean tissue growth. As a result of a high lean tissue growth, fat deposition is lower and feed conversion is better for GY pigs. It can be concluded that differences in performance due to breed are partly related to differences in feed intake pattern.

Between sexes the differences in feed intake pattern were not very strong. Gilts had significantly more meals and less feed intake per visit than boars. Therefore, it may be expected that lean percentage is higher for gilts. Probably the genetically determined maximum protein deposition has limited the protein growth. Because of a higher eating frequency at equal levels of daily eating time, gilts lost more energy with feed intake activity than boars. This may have contributed to a reduced production efficiency.

Heritabilities

Heritability estimates (Table 3) for production traits were somewhat higher than values reported in literature, especially growth rate and feed conversion (Standal and Vangen, 1983; Wyllie et al., 1979). Common environmental effect (litter) was small.

The heritability estimate for daily feed intake was in agreement with estimates in literature, concerning (semi) ad libitum feed intake (Standal and Vangen, 1983; Wyllie et al., 1979). No heritability estimates for FID based on group housing of pigs could be found, only of two pigs/pen with semi ad libitum feeding (Standal and Vangen, 1983). Heritability estimates for feed intake traits were lower than heritabilities for production traits. Number of meals and visits per day and feed intake per visit and per meal had moderate heritabilities of 0.35 to 0.49. Common environmental effect was large for daily feed intake, daily eating time and rate of feed intake. This shows that there is a strong litter effect on daily feed intake and rate of feed intake, possibly due to common litter behaviour during rearing.

Conclusions

A significant breed effect on all feed intake pattern traits was found, except for daily feed intake. Differences in feed intake pattern can partly be related to differences in growth performance between DL and GY pigs. A genetically determined high protein deposition for GY pigs, together with small meal sizes will have a positive effect on lean tissue formation. As reported by Henken (1991), GY pigs may have a low level of activity. This makes it possible to use more energy for lean deposition. As a result, daily weight gain and feed conversion were better for GY than DL pigs. In this study, differences in feed intake activity between GY and DL pigs could not be shown, as frequency of eating was higher for GY pigs, but daily eating time was less.

Heritability of daily feed intake was 0.16. The feed intake traits describing meal size and meal frequency (FIV, FIM, NVD, NMD) had moderate heritabilities between 0.35 and 0.49.

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REFERENCES

Batterham, E.S. and Bayley, H.S., 1989. Effect of frequency of feeding of diets containing free or protein bound lysine on the oxidation of [^{14}C]lysine or [^{14}C]phenylalanine by growing pigs. Br. J. Nutr., 62:647-655.

Bergström, P.L. and Kroeske, D., 1968. Methods of carcass assessment in research on carcass quality in the Netherlands. I. Description of the methods. EAAP Meeting Dublin; IVO-report C-123, Zeist, The Netherlands.

Campbell, R.G., Taverner, M.R. and Curic, D.M., 1985. Effects of sex and energy intake between 48 and 90 kg live weight on protein deposition in growing pigs. Anim. Prod.,40:497-503.

Campbell, R.G. and Taverner, M.R., 1988. Genotype and sex effects on the relationship between energy intake and protein deposition in growing pigs. J. Anim. Sci., 66:676-686.

De Haer, L.C.M., Luiting, P. and Aarts, H.L.M., 1992a. Relationships between feed intake pattern and residual feed intake in group housed growing pigs. Livest. Prod. Sci. (submitted).

De Haer, L.C.M., and Merks, J.W.M., 1992. Patterns of daily feed intake in growing pigs. Anim. Prod. 54 (in press).

De Haer, L.C.M., Merks, J.W.M., Kooper, H.G. and Van Hattum, J.A., 1992b. A note on the IVOG®-station: a feeding station to record the individual feed intake of group housed growing pigs. Anim. Prod. 54 (in press).

De Haer, L.C.M., and De Vries, A.G., 1992. Feed intake patterns and feed digestibility of growing pigs housed individually or in groups. Livest. Prod. Sci. (accepted).

Den Hartog, L.A., Verstegen, M.W.A. and Huisman, J., 1989. Amino acid digestibility in pigs as affected by diet composition. In: Friedman, M. (Editor), Absorption and utilization of amino acids, Vol. III., CRC Press, Florida, pp. 201-216.

Harvey, W.R., 1977. User's guide for LSML76 (Mixed Model Least Squares and Maximum Likelihood Computer Program). Mimeo, Ohio State University, 76 pages.

Henken, A.M., Van der Hel, W., Brandsma, H.A. and Verstegen, M.W.A., 1991. Differences in energy metabolism and protein retention of limit-fed growing pigs of several breeds. J. Anim. Sci., 69:1443-1453.

Krieter, J. and Kalm, E., 1989. Growth, feed intake and mature size in Large White and Pietrain pigs. J. Anim. Breed. Genet., 106:300-311.

Luiting, P., 1991. The value of feed consumption data for breeding in laying hens. Thesis Agricultural University Wageningen, The Netherlands, pp. 115-137.

Metz, S.H.M., Bergström, P.L., Lenis, N.P., De Wijs, M. and Dekker, R.A., 1980. The effect of daily energy intake on growth rate and composition of weight gain in pigs. Livest. Prod. Sci., 7:79-87.

Meyer, K., 1989. Restricted Maximum Likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. Genet. Sel. Evol., 21:317-340.

Owen, J.B., 1990. Weight control and appetite: nature over nurture. Anim. Breed. Abstr., 58(7):583-591.

Standal, N. and Vangen, O., 1983. Genetic variation in voluntary feed intake, correlation with other traits. 34th Annual Meeting of the European Association of Animal Production, Madrid, Spain, 12 pp.

Sundstøl, F., Standal, N. and Vangen, O., 1979. Energy metabolism in lines of pigs selected for thickness of backfat and rate of gain. Acta Agric. Scand., 29:337-345.

Van Kempen, G.J.M., Boer, H., Van der Poel, A.F.B. and Van Poppel, F.J.J., 1979. Effect of frequency of feeding and dietary treatment on metabolism, performance and carcass characteristics of swine. Neth. J. Agric. Sci., 27:199-210.

Walstra, P., 1987. The instrumental classification and grading of pigs in the Netherlands. Workshop "Experiences in Europe about porc objective grading", Reggio Emilia.

Wyllie, D., Morton, J.R. and Owen, J.B., 1979. Genetic aspects of voluntary food intake in the pig and their association with gain and food conversion efficiency. Anim. Prod., 28:381-390.

GENERAL DISCUSSION

GENERAL DISCUSSION

INTRODUCTION

The main aim of the present series of studies was to investigate relationships between feed intake pattern and production traits in growing pigs. Commercial fattening pigs are kept in groups, whereas station testing of pigs is mainly performed under individual housing. Therefore, the effect of housing system on feed intake pattern and production traits was investigated. Individual data about daily feed intake and feed intake pattern were recorded of individually and group housed pigs. Genetic parameters of feed intake pattern, like heritabilities and breed and sex effects on feed intake pattern were estimated.

Substantial differences in feed intake behaviour between individual and group housing systems were found. These were assumed to be associated with social interactions between animals. Furthermore, certain traits of intake behaviour were related with performance. Knowledge of these differences and relationships can be an explanation for possible genotype x housing system (GxH) interactions, if each genotype reacts differently on social interactions (like the establishment of a ranking order).

Relationships between feed intake pattern and performance can be derived from effects of eating behaviour on the utilisation of nutrients. The first possible effect may be through variation in digestion. Gross energy utilisation is different if feed digestibility is different. Furthermore, level of activity can affect the utilisation of absorbed energy for production and maintenance purposes. Protein utilisation will be influenced both by effects of feed digestibility on available amino acids and by the availability of essential amino acids throughout the day.

Therefore, subjects to be addressed in this discussion are:

1) Effects of housing system on feed intake pattern and production traits.
2) Effect of feed intake pattern on production traits.
3) Genetic aspects of feed intake pattern.

1. EFFECTS OF HOUSING SYSTEM

Feed intake behaviour

Feed intake patterns were derived from recordings of the individual feed intake in individual and group pens with IVOG-stations (De Haer et al., 1992b). To group visits to the feeding station into meals, a meal criterion of 5 minutes was used (De Haer and Merks, 1992). The Linda-index (De Haer and Merks, 1992; De Jong, 1985) was used to select the largest meals per day, that had a major contribution to daily feed intake.

The feed intake pattern in individual and group housing was described in Chapter 2 (De Haer and Merks, 1992). Feed intake patterns were significantly different when individual and group housing were compared. In group housing the daily number of visits and meals and daily eating time were lower than for individually housed pigs. Daily feed intake was not significantly different between the two housing systems. Duration of and feed intake per visit and per meal were higher and the rate of feed intake was higher for pigs housed in groups compared with individually housed pigs. The Linda-index was especially relevant for individual housing data, where this index indicated that 61% of the meals were very small, accounting for only 10% of the daily feed intake.

In groups, social interactions can increase activity level. Two kinds of social influences are present in group pens: social facilitation and agonistic behaviour (Hansen et al., 1982). The first effect has a positive effect on eating (stimulation of eating by seeing other pigs eating) and causes peaked distributions of feed intake activity (De Haer and Merks, 1992). The second effect (competition) results in less daily eating time and less frequent visits to the feed hopper in groups compared with individual pens (De Haer and Merks, 1992), and in a reduced daily feed intake for subordinate animals. Subordinate animals that are subjected to repeated biting, will generally become less active, reducing feed intake activity and daily feed intake and refraining from social activities (Fraser, 1973). Dominating pigs will have a higher daily eating time compared to subordinate pigs, as they eat most and they may occupy the feeder without eating (Hansen et al., 1982; Király and Wittmann, 1982). Ranking order is positively correlated with daily weight gain (Beilharz and Cox, 1967; Hansen et al, 1982; Király and Wittmann, 1982) and negatively correlated with lean percentage, though the lean percentage for the highest ranking pig is usually higher than for number two (Király and Wittmann, 1982).

In an experiment with two types of feeding stations with ad libitum feed intake (Molenaar, 1991, pers.com.), the effect of competition on feed intake pattern was studied. Two systems were compared: (1) a feeding station where the access to the feed hopper was limited and where a pig was protected when it was eating; (2) a feeding station with less protection and more competition.

In the first station the number of meals per day and the rate of feed intake were lower and the meal sizes were larger compared to the second system. This indicates that when there is less competition the pig can eat more slowly like in individual housing. A pig eating from station (1) will also increase its meal sizes, because it can eat protected and once out of the feeding station it is more difficult to come back.

Production traits

Housing system significantly affects production traits. In group housing daily weight gain and ultrasonic backfat thickness were lower and lean percentage was slightly higher than in individual housing. Feed conversion was not significantly different between the two housing systems (De Haer and De Vries, 1992a). Digestibility coefficients for dry matter were significantly lower for group housed pigs (Oude Elferink et al., 1986; De Haer and De Vries, 1992a), possibly negatively influenced by the large meal sizes and low frequency of eating in groups.

Differences in performance may be explained by health effects and by social effects. In group housing, infection pressure will be higher than in individual housing and injuries may be caused by pen mates. This will influence performance, as a (sub-)-clinical infection will have a negative effect on availability of energy and protein for weight gain. In our experiments 5% of the group housed pigs died from tail biting. A large proportion of pigs that finished the test (with a weight of 80 kg or more) were tail bitten too (5-15%).

In individual housing, a high daily gain and increased fatness may result from a low level of activity compared to group housing of pigs, as no social interactions are possible. An other reason may be the higher digestibility coefficients, due to more and smaller meals, which will increase daily gain. Patterson (1985) concluded, that a high growth rate and more backfat was primarily due to less metabolic heat produced by individually housed pigs compared to group housed pigs. Apparently, group housed animals produce more heat on the same level of feed intake. Patterson also indicated, that individually housed pigs may have elevated corticosteroid hormone levels, due to increased emotional stress. These elevated hormone levels will lower the retention of nitrogen by increased protein catabolism and, therefore, fatness can be increased.

Housing system significantly influenced correlations of digestibility coefficients with feed intake pattern (De Haer and De Vries, 1992a). Correlations between daily feed intake and production traits as estimated in group housing were lower than in individual housing (De Haer, unpublished results). These differences in correlations can be due to increased variance of energy losses related to activity (De Haer et al., 1992a), as a result from social interactions.

A high expression of genetic variation is preferred, which gives better possibilities to distinguish between animals. In group housing the expression of genetic variation is probably higher, as reported by De Haer (1990). In this study, heritability estimates in group housing were higher than in individual housing. This was due to increased sire variances in group housing compared to individual housing, whereas no large differences in error variances between the two housing systems were found. McBride et al. (1964) and Jonsson (1987) estimated an increased variance in growth rate in group housing compared with individual housing and they indicated that heritability estimates will depend on housing system. Furthermore, they suggested that social behaviour may give rise to GxH interactions.

Evidence for genotype x housing system interactions

Arguments for GxH interactions are reported in this thesis. Feed intake pattern is genetically determined and is significantly influenced by breed and sex. Through effects on feed intake behaviour, housing system influences level and variance of performance traits. In groups, ranking based on performance will be influenced by social ranking. Significant differences between correlations of digestibility with feed intake pattern in group housing and individual housing exist (De Haer and De Vries, 1992a).

Differences in genetic variances between housing systems will cause pseudo-interactions. These pseudo-interactions are due to differences in genetic scale, but not due to differences in ranking on performance of tested animals. Therefore, for animal breeding these pseudo-interactions are not important, but estimations of GxE interactions should be corrected for this effect (Dickerson, 1962). Different correlations within each housing system may cause GxH interactions, as genetic expressions are influenced by housing system, but probably not in the same way for each genotype. Estimations of GxH interactions may be biased by omitting data. Pigs ending the test prematurely (often 5 to 10% in group housing, but less in individual housing) by disease or death, are usually not included in the data set. Because of this effect possible GxH interactions are underestimated, as the genotypes that react strongest on differences in housing system are excluded from the data set.

However, the fact that differences in relationships between feed intake pattern and performance exist between the two housing systems, also indicates that, till a certain limit, pigs have the capacity to adapt to new circumstances. By changing hormone and enzyme secretions, digestion may not be influenced by differences in feed intake pattern (Low, 1989; Xu et al., 1991). When the adaptation to change in feed intake pattern, caused by differences in housing system, is similar for all pigs, GxH interactions due to digestive capacity will not occur.

In literature moderate genetic relationships are reported between central test data and progeny performance in different levels of a breeding programme (Standal, 1977; Ketelaars, 1979; Merks, 1989). In other studies results in different environments were more related, with no evidence for genotype x environment (GxE) interactions (Van Diepen and Kennedy, 1989; Crump et al., 1990).

Indications in for GxH interactions, as a possible component of GxE interactions, are not strong in literature. Genotype x testing regime interactions (De Haer, 1990), in which testing regime was a combination of housing system, sex and duration of test, were found to be of minor importance. Jonsson (1987), reviewing Danish and French research about GxH interactions, reported no significant GxH interactions, except for growth rate in one French breed.

From the discussion above it can be concluded, that there are theoretical reasons that GxH interactions exist, but GxH interactions are not significantly demonstrated. Therefore, GxH interactions are probably of minor importance. It may be possible that pigs adapt to different housing systems in the same way, without a great influence on genetic ranking of the pigs.

2. EFFECT OF FEED INTAKE PATTERN ON PERFORMANCE

Digestibility

Pigs with many meals of limited size may have a more continuous flow of digesta through the intestine (Ruckebusch and Bueno, 1976) and an increased amylase production, whereas lipase secretion is reduced (Hee et al., 1988). Gastric emptying (number of gushes) increases with increasing meal size. The amounts of dry matter and liquid emptied are greater with a larger meal (Gregory, McFayden and Rayner, 1990; Low, 1989; Sissons and Jones, 1991). Gastrin is a hormone that positively influences digestion through stimulation of acid secretion in the stomach and proliferation of mucosa in the gastro-intestinal tract. When feed intake per meal is high, gastrin secretion is increased (Xu et al., 1991). At a higher passage rate, especially through the large intestine, the efficiency of digestion can be reduced when there is also less fermentation in the hind gut (Van Es, 1982).

In group housing De Haer and De Vries (1992a) reported positive correlations between number of large meals per day and digestibility coefficients for crude protein and dry matter. In individually housed animals the number of visits per day to the feeder trough was significantly positively related with digestibility. Proportionately more large meals (group housing) and proportionately more visits per meal (both housing systems) were related with better digestibility. In individual housing daily eating time was negatively related with digestibility and an optimum rate of feed intake existed for maximum digestibility, which was slightly higher than the average rate of feed intake. In individual housing conditions, Van Kempen et al. (1979) found slightly increased digestibility coefficients at increased feeding frequency. From the results it can be concluded, that an increased frequency of eating, preferably within meals, is positively related with digestibility.

Positive correlations between digestibility coefficients, growth rate and backfat thickness were reported by Sundstøl et al., (1979), Wilmink (1979), Wenk and Morel

(1985) and De Haer and De Vries (1992a), and negative correlations of digestibility with feed conversion were found by De Haer and De Vries (1992a).

These relationships indicate, that in group housing pigs with many large meals and many visits clustered into meals, will have a better digestion of the feed and a better growth rate than pigs with few large meals. Proportionately more visits within a meal were positively related with digestibility. When relatively more visits are grouped in one meal, they have occurred with small time intervals between them. Concluding, when many visits were spread out over the day (large time intervals), digestibility was not improved.

Quantification

To quantify the effects of feed intake pattern traits on digestibility coefficients in group housing, regressions of digestibility on one standard deviation change of feed intake traits were calculated. Consequences of the effects on digestibility for available energy were estimated. The four strongest correlations (De Haer and De Vries, 1992a), between the digestibility coefficient for dry matter (DCdm) and feed intake pattern were used and a linear relationship between these traits was assumed.

Data:

Mean and standard deviation of DCdm: 0.71 ± 0.019
Mean of daily feed intake: 1995 g
ME feed = DE feed × 0.96 (NRC, 1988)

TABLE 1. Standard deviations of some feed intake pattern traits and correlation coefficients with the digestibility coefficient for dry matter (DCdm).

Trait	Correlations (r) with DCdm	St.dev.
Number of visits/day (NVD)	0.22	5.22
Number of large meals/day (NLX)	0.28	2.08
Number of meals per day	0.12	2.77
Time per visit (TV)	-0.11	1.35

Results:

The effect of increase of one standard deviation unit of feed intake pattern traits on digestibility will be equivalent to $(r \times 0.019/0.71) \times 0.96 \times 1995$ g more available feed:

5.22 more visits/day ≡ + 11.28 g feed

2.77 more meals/day ≡ + 6.15 g feed

2.08 more large meals/day ≡ + 14.35 g feed

1.35 more minutes/visit ≡ - 5.64 g feed

These results suggest, that pigs with 5.22 more visits per day, 2.77 more meals or 2.08 more large meals per day or 1.35 less minutes per visit (increase of one standard deviation unit) will have better digestibility coefficients, resulting in an increased availability of nutrients comparable with 11.28, 6.15, 14.35 or 5.64 g/d extra feed, respectively. This may accumulate to about 0.6 to 1.5 kg more available feed in the whole fattening period.

Activity

Feed intake activity may affect energy losses due to heat production. This energy can not be used for tissue formation. In growing pigs activity related heat production can amount 8% to 20% of the total heat production, depending on weight and feeding level (Verstegen et al., 1982). Halter et al. (1979) showed that activity increased total heat production by 10% to 17% and maintenance requirements by 18% to 25% for ad libitum fed piglets.

Residual Feed Intake (RFID=average residual daily feed intake) was defined as the difference between the observed feed intake of an animal (FID=daily feed intake) and its predicted feed intake (pFID) (Foster et al., 1983; Luiting and Urff, 1987). For growing pigs, pFID was represented by average metabolic body weight during test, average daily weight gain and IVO lean percentage at the end of test (De Haer et al., 1992a). 32% Of the variation in FID was explained by these covariables describing pFID and by fixed effects.

RFID is a measure of net efficiency of an animal (Luiting, 1991). Luiting et al. (1991) showed that especially physical activity in laying hens was highly positively correlated with RFID. In addition, Braastad and Katle (1989) showed that feed intake activity in laying hens was positively related with RFID. De Haer et al. (1992a) showed that variation in feed intake activity, described by daily eating time and frequency of eating, accounted for 47% of the variation in RFID. Pigs with a lower RFID had less visits and meals and spent, therefore, less time eating per day than pigs with a high RFID. Furthermore, these pigs had proportionately less visits within a meal, indicating that the visits were more spread out over the whole day. The fraction of large meals was higher. Pigs with a high predicted FID, and thus high production level, had a high rate of feed intake. Nienaber and Hahn (1987) showed that heavy pigs had 50% less meals than light weight animals, when both groups had started the test with the same average weight. Conclusively, the more efficient animals were animals with reduced feed intake activity.

A systematically performed physical exercise on a moderate level in rats, had some influence on resting metabolic rate (5% increase) (Keller and Janji, 1991). Comparable results were reported for humans (Poehlman and Horton, 1989). This indicates that activity will not only increase heat production during the moments of movement, but that some animals also have higher maintenance requirements when they are not active. Level of maintenance requirements per kg metabolic body weight seems to be related to the environment of the animal. This is supported by Grimbergen (1974), who showed with laying hens that differences in environmental conditions affect maintenance requirements. Experiments under practical conditions resulted in higher maintenance requirements per kilogram metabolic body weight than experiments in metabolism cages.

Quantification

To quantify the importance of variation in maintenance requirements for the daily feed requirements, we assume that average daily feed intake is 1995 g, or 25.935 MJ (= 1.88 times maintenance). Average maintenance requirements per kg metabolic weight are assumed to be 460 kJ, with a coefficient of variation of 20% (NRC, 1988). At an average metabolic body weight during test of 25.6 kg, an increase of one standard deviation unit of maintenance requirements/kg$^{0.75}$ will increase daily energy requirements with 9% $(=460 \times 0.20 \times 25.6 \times 100\% / 25935)$, equivalent to 181 g more feed required per day.

The effect of feed intake pattern on RFID in group housing was quantified, by using strongest correlations of feed intake traits with RFID (De Haer et al., 1992a). The regression of one standard deviation increase of a feed intake trait on RFID was calculated, assuming a linear relationship.

Data:

Residual daily feed intake (RFID): 0.0 ± 218 g

Mean of daily feed intake: 1995 g

TABLE 2. Standard deviations of some feed intake pattern traits and correlation coefficients with residual daily feed intake (RFID).

Trait	Correlations (r) with RFID	St.dev.
Number of visits/day (NVD)	0.51	5.22
Number of meals/day (NMD)	0.45	2.77
Number of large meals/day (NLX)	0.31	2.08
Eating time per day (TD)	0.64	10.8

Results:

The effect of increase of one standard deviation unit of feed intake pattern traits on RFID will be equivalent to $r \times 218$ g more feed required at the same production level:

5.22 more visits/day ≡ + 111.2 g feed

2.77 more meals/day ≡ + 98.1 g feed

2.08 more large meals/day ≡ + 67.6 g feed

10.8 more minutes/day ≡ +139.5 g feed

From these results it is concluded that pigs with 5.22 more visits, 2.77 more meals, 2.08 more large meals or 10.8 min more eating time per day will need 111.2, 98.1, 67.6 and 139.5 g/d feed more, respectively. These feed requirements represent energy losses due to activity and energy gains due to a better digestibility, independent of production level. It can be concluded, that the effect of an increased frequency of eating on energy losses due to activity is higher than the effect on energy gains due to a better digestibility.

Availability of amino acids

Proportionately 0.66 to 0.68 of the total amount of protein that is absorbed within 5 h. is absorbed during the first 2 h. (Rérat and Corring, 1991). Amino acids in the blood are rapidly removed when they are not utilised and it is thought that they may be broken down. At a high eating frequency (a more balanced supply over the day) the availability of essential amino acids will be improved (Batterham and Bayley, 1989; Den Hartog et al., 1989), resulting in an increased nitrogen retention (Fábry, 1967). However, a positive effect of eating frequency on growth rate was not found, probably due to increased energy losses when frequency of eating is increased (De Haer et al., 1992a). It is not known whether an increased availability of amino acids in our experiments may have an effect on lean tissue growth. More basic research is needed, to quantify relationships between eating frequency, availability of amino acids and lean tissue formation.

Final remark

In this research we always looked at the effect of feed intake pattern on performance, but strictly speaking we can not conclude whether feed intake pattern is a cause or a consequence of performance.

3. GENETIC ASPECTS OF THE FEED INTAKE PATTERN

Genetic effects and relationships

Group housing compared to individual housing has the advantage that possible GxH interactions are minimised and housing costs per pig place are lower. This offers possibilities for increased testing capacity. In group housing significant correlations between feed intake pattern and efficiency of production were found (De Haer et al., 1992a). These relationships indicate negative relations of daily eating time and eating frequency with efficiency (represented by RFID). Relations of meal size and rate of feed intake with lean percentage were negative, with daily gain they were positive. Heritability estimates for feed intake traits were moderate to low (De Haer and De Vries, 1992b), with heritabilities of 0.35 to 0.49 for meal size and frequency of eating (FIV, FIM, NVD, NMD, NLX).

Feed intake pattern may add extra information about production efficiency, represented by RFID. As was shown by De Haer et al. (1992a), the feed intake pattern has much stronger correlations with RFID than with the feed intake required for the production level. As it is difficult to measure RFID and correlations of TD and NVD with RFID are high, the feed intake pattern may be a useful tool for selecting a more efficient pig. In mice, selection for high daily feed intake resulted in higher maintenance requirements per kg metabolic body weight and an increased daily gain (Bishop and Hill, 1985; Notter and Wyatt, 1991). In pig production, maintenance requirements account for about 40% of total energy intake. Selection for low maintenance requirements per kg metabolic body weight may offer possibilities for improvement of daily gain and production efficiency. A pig should be selected for a low appetite for RFID (in which variation in maintenance requirements due to activity is included), but a high appetite for production (weight gain). In fact, this is shown when boars and gilts are compared. Chadd and Cole (1988) indicated, that despite a lower daily feed intake, boars had a higher daily weight gain and better feed efficiency than gilts.

A trait that was not investigated in this thesis, but that may also offer information about performance, is a daily feed intake curve during test. Young pigs have a relatively higher potential for protein deposition than older pigs. Maybe selection should be directed towards pigs with a high daily feed intake in the beginning of test and a relatively lower daily feed intake in the second part of the test. This means, that the curve should start with a steep line, that levels off within a few weeks.

Feed intake traits that are highly correlated with daily feed intake are eating time per day ($r=0.55$) and number of visits per day ($r=0.38$). When pigs are tested in groups, recordings of eating time and/or frequency of eating can be used instead of feed intake recording, which will reduce equipment costs by about 35%.

Grouping of visits into meals and meals into large meals did not greatly increase correlations with production traits and RFID (De Haer et al., 1992a). Therefore, feed intake per visit, number of visits per day, rate of feed intake and eating time per day can be chosen as traits that are highly correlated with production and RFID. Grouping into meals and large meals did provide more information about the daily distribution of meals in animals with a low and a high RFID (De Haer et al., 1992a). Low RFID was related with a low proportion of visits within meals and a high fraction of large meals. Large differences in proportion of visits per meal and fraction of large meals were shown between individual and group housing (De Haer and Merks, 1992).

Selection with and without information on feed intake and feed intake pattern

In index selection all available data are combined in an index of merit. The index is the best linear prediction of an individuals breeding value, in the form of a multiple regression of breeding value on all sources of information. The index of each individual is represented by:

$$I = b_1P_1 + b_2P_2 + b_3P_3 + \ldots + b_nP_n \quad (1)$$

where: I = selection index; P_n = phenotypic value of the individual for daily weight gain, backfat thickness or daily feed intake (the latter can be omitted or replaced by feed intake pattern traits), as deviations from the contemporary mean.

Based on De Roo (1988), the following aggregate genotype was assumed:

$$H = 0.178A_1 - 0.05A_2 + 3.0A_3 \quad (2)$$

where: H = breeding goal; A_1 = daily weight gain (g/d); A_2 = daily feed intake (g/d); A_3 = IVO lean percentage.

In the breeding goal daily feed intake (FID) is included. Accuracy of selection is highest when FID is included in the selection index. Individual FID in group housing can be measured with feeding stations. As it is cheaper to measure individual number of visits per day (NVD) and daily eating time (TD) than FID, an alternative for selection on FID can be to measure TD and NVD or one of these traits.

Table 3. Genetic and phenotypic parameters of production traits and feed intake pattern traits that are used for index selection evaluations. h_1^2 and h_2^2 are estimated heritabilities and assumed heritabilities, respectively.

Trait	st.dev.	h_1^2	h_2^2
Daily weight gain (WG)	72.3	0.49	0.49
Daily feed intake (FID)	0.263	0.16	0.25
IVO lean percentage	2.2	0.55	0.55
Backfat thickness (BT)	1.7	0.57	0.57
Daily eating time (TD)	10.8	0.24	0.25
Number of visits/day (NVD)	5.2	0.38	0.25

With the computer program SELIND selection results were calculated, including FID, NVD or TD in the selection index. Correlations between index traits and aggregate genotype traits are reported in Chapter 4. As genetic correlations were not estimated, they were set equal to phenotypic correlations.

Table 4. Predicted selection responses for daily weight gain (WG), daily feed intake (FID) and IVO lean percentage, based on own performance data for WG, ultrasonic backfat thickness (BT) and feed intake pattern traits. On the first line, results are based on estimated heritabilities, on the second line heritabilities for FID and feed intake traits are assumed to be 0.25.

Selection traits	r_{IH}	Genetic gain		
		WG (g/d)	FID (g/d)	IVO (%)
WG, BT	0.454	26.3	18.3	0.06
	0.406	23.8	18.9	0.16
WG, FID, BT	0.546	26.6	0.38	0.02
	0.553	21.3	-18.8	0.12
WG, NVD, BT	0.490	24.1	5.8	0.09
	0.441	21.3	5.1	0.18
WG, TD, BT	0.490	24.2	5.9	0.09
	0.461	20.6	-1.3	0.17
WG, TD, NVD, BT	0.503	23.5	1.6	0.10
	0.468	20.1	-4.0	0.18

From Table 4 it is concluded, that including FID in the selection index increases accuracy of selection by 20% (resp. 36% when h^2 for FID = 0.25). When FID is not measured, including TD in the selection index with WG and BT increases genetic progress by 8% (resp. 9%) and including NVD increases genetic progress by 8% (resp. 14%). When TD and NVD together are included in the selection index instead of FID, genetic progress is increased by 11% (resp. 15%). When TD and NVD are added to the selection index with FID, WG and BT, genetic progress is not improved (+0.4%) compared to selection on FID, WG and BT.

When heritabilities of FID and other feed intake traits are set to 0.25, differences between results with various selection indices become larger.

GENERAL CONCLUSIONS

Large differences in feed intake pattern and performance are found between individual and group housing, but it was concluded that genotype x housing system interactions are of minor importance. This indicates that housing system influences different genotypes of pigs to a similar level. No differences in genetic ranking order based on performance results is expected. Pseudo-interactions may result from increased variation in production traits in group housing.

In group housing, significant correlations of feed intake pattern with growth performance and efficiency of production are reported. Number of visits per day and daily eating time are strongly positively related with level of activity and, therefore, negatively related with efficiency of production. Rate of feed intake and meal size are positively related with production level, especially with daily gain. Number of large meals per day and number of visits within a meal are positively related with digestibility of the feed. However, a reduction in number of visits per day is energetically more beneficial due to a reduced level of activity.

Feed intake pattern was partly genetically determined, with moderate heritabilities. Significant breed and sex effects on feed intake pattern were found. Level of activity and maximum potential level of protein deposition may differ between breeds. These effects may influence relationships between feed intake pattern and performance.

Compared to a selection index with daily weight gain and ultrasonic backfat thickness, adding individual daily feed intake will result in about 20 to 36% genetic progress more. Not measuring individual daily feed intake, but using data about individual daily eating time and number of visits per day, will increase genetic progress by 8 to 15%.

REFERENCES

Batterham, E.S. and Bayley, H.S., 1989. Effect of frequency of feeding on the efficiency of protein utilization of cattle. Ind. J. Anim. Nutr., 6(2):126-131.

Beilharz, R.G. and Cox, D.F., 1967. Social dominance in swine. Anim. Behav., 15:117-122.

Braastad, B.O. and Katle, J., 1989. Behavioral differences between laying hen populations selected for high and low efficiency of food utilization. Br. Poultry Sci., 30:533-544.

Bishop, S.C. and Hill, W.G., 1985. Effects of selection on growth, body composition and food intake in mice. III. Correlated responses: growth, body composition, food intake and efficiency and catabolism. Genet. Res., Camb., 46:57-74.

Chadd, S.A. and Cole, D.J.A., 1988. Appetite, growth and carcass characteristics of modern pig genotypes. Proc. VIth World Conference on Animal Production, Helsinki, Finland, p. 438.

Crump, R.E., Thompson, R. and Mercer, J.T., 1990. The genetic relationship between sexes for pig performance traits as recorded in a commercial Landrace nucleus herd. 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, United Kingdom, XV:454-457.

De Haer, L.C.M. and De Vries, A.G., 1992a. Feed intake patterns and feed digestibility of growing pigs housed individually or in groups. Livest. Prod. Sci. (accepted).

De Haer, L.C.M. and De Vries, A.G., 1992b. Genetic aspects of the feed intake pattern of group housed growing pigs. Livest. Prod. Sci. (submitted).

De Haer, L.C.M., Luiting, P. and Aarts, H.L.M., 1992a. Relationships between individual residual feed intake and feed intake pattern in group housed growing pigs. Livest. Prod. Sci. (submitted).

De Haer, L.C.M. and Merks, J.W.M., 1992. Patterns of daily feed intake in growing pigs. Anim. Prod., 54 (in press).

De Haer, L.C.M., Merks, J.W.M., Kooper, H.G. and Van Hattum, J.A., 1992b. A note on the IVOG®-station: a feeding station to record the individual feed intake of group housed growing pigs. Anim. Prod., 54 (in press).

De Jong, H.W., 1985. Dynamische Markttheorie. Stenferd Kroese B.V., Leiden, The Netherlands, pp. 23-24.

Den Hartog, L.A., Verstegen, M.W.A. and Huisman, J., 1989. Amino acid digestibility in pigs as affected by diet composition. In: Friedman, M. (Editor), Absorption and utilization of amino acids, Vol. III. CRC Press, Florida, pp. 201-216.

De Roo, G., 1988. Studies on breeding schemes in a closed pig population. 1. Population size and selection intensities. Livest. Prod. Sci., 19:417-444.

Dickerson, G.E., 1962. Implications of genetic-environmental interaction in animal breeding. Anim. Prod., 4:47-63.

Fábry, P., 1967. Metabolic consequences of the pattern of feed intake. In: Code, F.P. (Editor), Handbook of physiology, Sect. 6: Alimentary canal. American Physiological Society, pp. 31-49.

Foster, W.H., Kilpatrick, D.J. and Heaney, I.H., 1983. Genetic variation in the efficiency of energy utilization by the fattening pig. Anim. Prod., 37:387-393.

Fraser, D., 1973. The behaviour of growing pigs during experimental social encounters. J. Agric. Sci., Camb., 82:147-163.

Gregory, P.C., McFayden, M. and Rayner, D.V., 1990. Pattern of gastric emptying in the pig: relation to feeding. Br. J. Nutr., 64:45-58.

Grimbergen, A.H.M., 1974. Energy expenditure under productive conditions. In Morris, T.R. and Freeman, B.M. (Editors), Energy requirements of poultry, Br. Poultry Sci. Ltd., Edinburgh, Great Britain, pp. 61-71.

Halter, H.M., Wenk, C. and Schürch, A., 1979. Effect of feeding level and feed composition on energy utilization, physical activity and growth performance of piglets. In: Mount, L.E. (Editor), Proc. 8th Symposium on Energy Metabolism, Cambridge, Great Britain. EAAP publ. no. 26, Butterworths, London, pp. 395-398.

Hansen, L.L., Hagelsø, A.M. and Madsen, A., 1982. Behavioral results and performance of bacon pigs fed "ad libitum" from one or several self-feeders. Appl. Anim. Ethol., 8:307-333.

Hee, J., Sauer, W.C. and Mosenthin, R., 1988. The effect of feeding on the pancreatic secretions in the pig. J. Anim. Physiol. Anim. Nutr., 60:249-256.

Jonsson, P., 1987. Social ranking in pigs and its relation to genotype by environment interaction. World Rev. Anim. Prod., XXIII (4):33-38.

Keller, J.S. and Janji, G., 1991. Energy expenditure resulting from physical activity as influenced by dietary protein level and environmental temperature. 12th Symposium on Energy Metabolism of Farm Animals, Kartause Ittingen, Switzerland.

Ketelaars, E.H., 1979. De vererving van onder praktijkomstandigheden geregistreerde kenmerken bij varkens. Verslag Landbk. Onderz., 883. Pudoc, Wageningen.

Király, A. and Wittmann, M., 1982. The relationship of production traits with the order of hierarchy at fattening pigs. Proc. Res. Centre for Anim. Husb. Nutr., Gödöllö, Hungary.

Low, A.G., 1989. Research into the digestive physiology of pigs. In: Van Weerden, E.J. and Huisman, J. (Editors), Nutrition and digestive physiology in monogastric farm animals. Symposium on occasion of retirement Dr. E.J. van Weerden, Pudoc, Wageningen, The Netherlands, pp. 1-15.

Luiting, P. and Urff, E.M., 1987. Residual feed intake: a new source of genetic variation for feed efficiency. 38th Annual Meeting of the European Association for Animal Production, Lisbon, Portugal, GNC4.8: 6pp.

Luiting, P., 1991. The value of feed consumption data for breeding in laying hens. PhD thesis Wageningen Agricultural University, The Netherlands, pp. 115-137.

Luiting, P., Schrama, J.W., Van der Hel, W. and Urff, E.M., 1991. Metabolic differences between White Leghorns selected for high and low residual feed consumption. Br. Poultry Sci., 32:763-782.

McBride, G., James, J.W. and Hodgens, N., 1964. Social behaviour of domestic animals. IV. Growing pigs. Anim. Prod., 6:129-139.

Merks, J.W.M., 1989. Genotype x environment interactions in pig breeding programmes. VI. Genetic relations between performances in central test, on-farm test and commercial fattening. livest. Prod. Sci., 22:325-339.

Nienaber, J.A. and Hahn, G.L., 1987. Feeding behaviour and energetics of growing-finishing swine as influenced by environmental temperature. ASAE paper no. 87-4512. Michigan, U.S.A.

Notter, D.R. and Wyatt, W.E., 1991. Effects of genetic line and intake level on growth of mice: feed intake and mature maintenance requirements. J. Anim. Breed. Genet., 108:299-314.

NRC, 1988. The nutrient requirements of swine. 9th Revised Edition, National Research Council. National Academy Press, Washington D.C., U.S.A., 93 pp.

Oude Elferink, G., Mentink, A., Everts, H., Smits, B. and Jongbloed, A.W., 1986. Digestibility in swine depending on several factors: literature research and report of a number of trials. Report no. 174, IVVO, Lelystad, The Netherlands.

Patterson, D.C., 1985. A note on the effect of individual penning on the performance of fattening pigs. Anim. Prod., 40:185-188.

Poehlman, E.T. and Horton, E.S., 1989. The impact of food intake and exercise on energy expenditure. Nutr. Rev., 47(5):129-137.

Rérat, A. and Corring, T., 1991. Animal factors affecting protein digestion and absorption. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no. 54, Pudoc, Wageningen, The Netherlands, pp. 5-34.

Ruckebusch, Y. and Bueno, L., 1976. The effect of feeding on the motility of the stomach and small intestine in the pig. Br. J. Nutr., 35:379-405.

Sissons, J.W. and Jones, C.L., 1991. Ultrasonic and electromyographic measurements of the effects of feed intake on digesta flow and gastro-intestinal motility in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, L.A. (Editors), Proc. Vth Int. Symposium on Digestive Physiology in pigs. EAAP publ. no. 54, Pudoc, Wageningen, The Netherlands, pp. 120-125.

Standal, N., 1977. Studies on breeding and selection schemes in pigs. VI. Correlation between breeding values estimated from station test and on-farm test data. Acta Agric. Scand., 27:138-144.

Sundstøl, F., Standal, N. and Vangen, O., 1979. Energy metabolism in lines of pigs selected for thickness of backfat and rate of gain. Acta Agric. Scand., 29:337-345.

Van Diepen, T.A. and Kennedy, B.W., 1989. Genetic correlations between test station and on-farm performance for growth rate and backfat in pigs. J. Anim. Sci., 67:1425-1431.

Van Es, A.J.H., 1982. Energy metabolism in pigs. A review. In: Ekern, A. and Sundstøl, F. (Editors), Proc. 9th Symposium on Energy metabolism in farm animals, Lillehammer, Norway. EAAP publ. no. 29, pp. 249-255.

Van Kempen, G.J.M., Boer, H., Van der Poel, A.F.B. and van Poppel, F.J.J., 1979. Effect of frequency of feeding and dietary treatment on metabolism, performance and carcass characteristics of swine. Neth. J. Agric. Sci., 27:199-210.

Verstegen, M.W.A., Van der Hel, W., Brandsma, H.A. and Kanis, E., 1982. Heat production of groups of growing pigs as affected by weight and feeding level. In: Ekern, A. and Sundstøl, F. (Editors), Proc. 9th Symposium on Energy metabolism in farm animals, Lillehammer, Norway. EAAP publ. no. 29, pp. 221-221.

Wenk, C. and Morel, P., 1985. Genetic variation of the digestibility of energy in growing pigs. Proc. 3rd. Int. Seminar on Digestive Physiology in the Pig. Copenhagen, Denmark, pp. 396-399.

Wilmink, H., 1979. Digestibility coefficients in lines of pigs selected for growth and backfat thickness. M.Sc. thesis, Dept. Anim. Breed., Wageningen Agricultural University, The Netherlands.

Xu, R.-J., Cranwell, P.D. and Hennessy, D.P., 1991. Effects of method of feeding and meal size on the postprandial gastrin response in pigs. In: Verstegen, M.W.A., Huisman, J. and Den Hartog, (Editors), Proc. Vth Int. Symposium on Digestive Physiology in Pigs. EAAP publ. no 54, Pudoc, Wageningen, The Netherlands, pp. 41-46.

SUMMARY

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Introduction

In pig breeding, potential breeding boars and gilts are usually tested on central test stations in individual pens. Commercial fattening pigs are kept in groups. Differences in housing system may contribute to genotype x environment (GxE) interactions by introducing genotype x housing system (GxH) interactions. In this study pigs were tested in individual and group housing. A feeding station was developed, the IVOG®-station, to enable recording of individual daily feed intake and feed intake pattern in each housing system.

The aim of this thesis was, to investigate differences in performance and feed intake pattern between individual and group housing. Further, in group housing relationships between feed intake pattern and performance were investigated and genetic aspects of the feed intake pattern were determined. Genetic aspects include estimation of heritabilities and differences between Dutch Landrace (DL) and Great Yorkshire (GY) pigs. Knowledge of these relationships and genetic aspects may be utilised for selection, when pigs are tested in group pens with individual recording of the feed intake pattern.

A description of the IVOG®-station is given in Chapter 1. Of each visit of a pig to the feed hopper, the animal identification number is recorded together with time and weight of the feed, at the beginning and at the end of the visit. The entrance to the feeder is open and competition among pigs for the feed is possible.

Effect of housing system on feed intake pattern and production traits

In Chapters 2 and 3, differences in feed intake pattern between individual and group housing are described. Intervals between visits to the feed hopper of 5 minutes or less (which was used as a meal criterion), were regarded as within-meal intervals and the visits were grouped into one meal. The so called Linda-index was used to select those meals, that had a major contribution to daily feed intake.

In individual pens daily eating time and frequency of eating (number of visits and number of meals per day) were higher than in group pens. Pigs in group pens had a higher feed intake per meal and per minute, and they spent more time per meal than individually housed pigs. Housing system did not significantly influence daily feed intake.

Housing system significantly influenced daily gain, backfat thickness and digestibility coefficients for dry matter. Pigs in individual pens had better digestibility coefficients and daily gain and more backfat compared with group housed pigs.

In the General Discussion it was derived, that some theoretical arguments for GxH interactions are present. Feed intake pattern traits are partly genetically determined. Further, in group housing level and variance of feed intake pattern and production traits are influenced by social interactions. Housing system also influenced relationships between feed intake pattern and performance. However, in literature little evidence for GxH interactions was found.

Relationships between feed intake pattern and production traits

In Chapter 3 individual digestibility coefficients were determined for dry matter (DCdm) and crude protein (DCcp). Within each housing system, relationships between feed intake pattern and digestibility coefficients were estimated. In individual housing digestibility was significantly negatively correlated with daily eating time. In group housing this correlation was almost zero and significantly different from the correlation in individual housing. In individual housing an optimum rate of feed intake was found for highest digestibility. In both housing systems number of visits per day was positively and time spent per visit was negatively related with digestibility. In group housing also number of large meals per day was significantly positively correlated with digestibility. The correlations indicated that frequency of eating and, in individual housing, rate of feed intake, were significantly related with digestibility.

Digestibility was positively related with daily gain and negatively related with feed conversion.

In Chapter 4, relationships between feed intake pattern and performance traits were investigated. Special attention was given to feed utilisation. Variation in daily feed intake among animals was explained for 32% by metabolic body weight, daily weight gain and IVO lean percentage. The difference between the observed daily feed intake and predicted feed intake was defined as residual daily feed intake (RFID). RFID consists of non-accounted energy and protein losses.

Rate of feed intake and feed intake per visit and per meal were significantly positively related with daily gain, backfat thickness and predicted feed intake, but negatively with lean percentage. A low daily eating time, few visits and meals and proportionately many visits per meal and a high feed intake per visit, were related with a low RFID and, therefore, with a high efficiency of production. Relationships between feed intake pattern and RFID existed through the effect of feed intake pattern on level of feed intake activity and on digestibility of feed.

In the General Discussion, the effects of feed intake pattern on digestibility and activity were quantified. Energetically, feed intake pattern had a stronger effect through level of activity than through digestibility of feed.

Genetic aspects of the feed intake pattern

In Chapter 5 it was shown that feed intake pattern traits have moderate to low heritabilities. Heritabilities were highest for traits describing frequency of eating and feed intake per visit or per meal. A significant breed effect was found on feed intake pattern and production traits. DL pigs had less visits and meals per day and more eating time and feed intake per visit and per meal than GY pigs. GY pigs had a higher rate of feed intake and less daily eating time per day than DL pigs, together with proportionately more large meals.

Daily gain and lean percentage were higher for GY than DL pigs, probably due to a higher maximum protein deposition and lower maintenance requirements per kg metabolic weight.

Impacts of recording feed intake on practical breeding programmes were predicted in the General Discussion. Including individual daily feed intake in a selection index with daily gain and backfat thickness will increase genetic progress by 20 to 36%. Substitution of daily feed intake with number of visits per day and daily eating time, will increase genetic progress by 11 to 15%.

Main conclusions

- Housing system significantly influences feed intake pattern, probably through social interactions between pen mates. Pigs in groups have larger meals, a higher rate of feed intake, less daily eating time and less meals per day compared to individually housed pigs. Daily feed intake is not significantly influenced by housing system.
- Housing system significantly influences digestibility coefficients, daily weight gain and backfat thickness. In individual housing, digestibility coefficients for dry matter, backfat thickness and daily weight gain were significantly higher than in group housing.
- Arguments for genotype x housing system interactions are found, but in literature evidence for GxH interactions is weak.
- Rate of feed intake and meal size are significantly positively related with daily weight gain and backfat thickness and negatively related with lean percentage.

- Daily eating time and frequency of eating are significantly negatively related with efficiency of production, through an effect on feed intake activity and digestibility. Energetically, the effect of feed intake pattern through level of activity is stronger than through digestibility of feed.
- Feed intake pattern traits have moderate to low heritabilities. Highest heritabilities were found for traits describing frequency of eating and meal size.
- Breed significantly influences feed intake pattern and level of activity and, therefore, maintenance requirements per kg metabolic body weight.
- Group-tested pigs may be selected with an index containing daily weight gain and backfat thickness. When individual daily feed intake is included in this selection index, genetic progress of breeding programmes will be 20 to 36% higher. When individual daily feed intake is not measured, but replaced by number of visits per day and daily eating time, genetic progress will be 11 to 15% higher. These results are only valid, when all genotypes are tested in groups and feed intake traits are recorded of all pigs.
- Testing of breeding pigs in group housing is less expensive and group housing is more comparable to practical conditions than individual housing. Not measuring individual daily feed intake will reduce genetic progress. Recording of daily eating time and frequency of eating may replace feed intake measurements, although genetic progress will be somewhat lower.

SAMENVATTING

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Inleiding

In de varkensfokkerij worden toekomstige fokberen en -gelten gewoonlijk getest op centrale toetsstations, in individuele huisvesting. Op de commerciële mesterijbedrijven worden varkens in groepshokken gehouden. Omdat genotype x huisvestingvorm (GxH) interacties kunnen optreden, kunnen verschillen in huisvestingssysteem bijdragen aan genotype x milieu (GxE) interacties. In dit onderzoek werden varkens getest in individuele en groepshuisvesting. Om de individuele voeropname en het voeropnamepatroon van varkens in elk huisvestingssyteem te registreren, werd een voerstation ontwikkeld, het IVOG®-station.

Het doel van dit onderzoek was, om bij varkens in individuele en groepshuisvesting verschillen in produktie-kenmerken en voeropnamepatroon te onderzoeken. Verder werden bij varkens in groepshuisvesting ook relaties tussen voeropnamepatroon en produktie-kenmerken onderzocht. Genetische aspecten van het voeropnamepatroon werden bepaald, wat inhield dat erfelijkheidsgraden werden geschat en verschillen in voeropnamepatroon tussen Nederlands Landras (NL) en Groot Yorkshire (GY) varkens werden bepaald. Wanneer erfelijkheidsgraden en relaties tussen voeropnamepatroon en produktie bekend zijn en fokvarkens getest worden in groepshuisvesting met individuele voeropnameregistratie, kunnen voeropnamekenmerken bij de selectie van fokvarkens gebruikt worden.

In Hoofdstuk 1 wordt een beschrijving gegeven van het IVOG®-station. Bij elk bezoek van een varken aan de voerbak wordt het diernummer geregistreerd, evenals het gewicht van het voer en de tijd aan het begin en het eind van het bezoek. De toegang naar de voerbak is altijd open en er is competitie om het voer tussen de varkens mogelijk.

Effect van het huisvestingssyteem op voeropnamepatroon en produktie-kenmerken

In de Hoofdstukken 2 en 3 worden verschillen in voeropnamepatroon tussen individuele en groepshuisvesting beschreven. Intervallen tussen bezoeken aan de bak, die korter waren dan 5 minuten (het zgn. maaltijd-criterium), werden beschouwd als binnen-maaltijd intervallen en de bezoeken werden in één maaltijd gegroepeerd. De zgn. Linda-index werd gebruikt om van alle maaltijden, de maaltijden met de grootste bijdrage aan de dagelijkse voeropname te kiezen.

In individuele huisvesting waren dagelijkse voeropnametijd en het aantal bezoeken en maaltijden per dag groter dan bij varkens in groepshuisvesting. Varkens in groepen hadden een hogere voeropname per bezoek, per maaltijd en per minuut en de tijd per bezoek en per maaltijd was hoger. Dagelijkse voeropname werd niet significant beïnvloed door het huisvestingssysteem.

Huisvestingssysteem had een significante invloed op dagelijkse groei, rugspekdikte en verteringscoëfficiënten voor droge stof. Bij varkens in individuele huisvesting waren de groei en vertering van droge stof beter, terwijl het rugspek dikker was.

In de Algemene Discussie wordt afgeleid, dat er aanwijzingen bestaan voor GxH interacties. Het voeropnamepatroon is namelijk deels erfelijk bepaald. Verder worden in groepshuisvesting niveau en varianties van kenmerken beïnvloed door sociale interacties. Relaties tussen voeropnamepatroon en produktie werden ook door huisvestingssysteem beïnvloed. In de literatuur werd echter nauwelijks bewijs gevonden voor het bestaan van GxH interacties.

Relaties tussen voeropnamepatroon en produktie-kenmerken

In Hoofdstuk 3 zijn verteringscoëfficiënten bepaald voor droge stof (DCdm) en ruw eiwit (DCcp). Binnen elk huisvestingssyteem zijn relaties tussen voeropnamepatroon en verteringscoëfficiënten bepaald. In individuele huisvesting werd een significant negatieve correlatie gevonden tussen vertering en dagelijkse voeropnametijd. In groepshuisvesting was deze relatie bijna nul en de correlatie was significant verschillend van de correlatie in individuele huisvesting. In individuele huisvesting was de hoogste vertering gecorreleerd met een optimale voeropnamesnelheid. In beide huisvestingssystemen waren aantal bezoeken aan de bak positief en tijd per bezoek negatief gerelateerd met vertering. In groepshuisvesting had ook het aantal grote maaltijden per dag een positieve correlatie met vertering. De correlaties lieten zien, dat voeropname frequentie en, in individuele huisvesting, voeropnamesnelheid, significant gerelateerd waren met vertering van het voer.

Er werd een positieve relatie gevonden tussen vertering en dagelijkse groei; de relatie tussen vertering en voederconversie was negatief.

In Hoofdstuk 4 werden relaties tussen voeropnamepatroon en produktie-kenmerken onderzocht. Er werd vooral gelet op voederbenutting. Variatie in dagelijkse voeropname werd voor 32% verklaard door metabolisch lichaamsgewicht, dagelijkse groei, en IVO vleespercentage. Het verschil tussen geregistreerde dagelijkse voeropname en de voorspelde voeropname (op grond van de genoemde kenmerken), was gedefinieerd als residuele dagelijkse voeropname (RFID). RFID bevat energie- en eiwitverliezen, die niet door het model verklaard worden.

Voeropnamesnelheid en voeropname per bezoek en per maaltijd hadden een significant positieve relatie met dagelijkse groei, rugspekdikte en voorspelde voeropname, maar een negatieve relatie met vleespercentage. Een lage voeropnametijd per dag, weinig bezoeken en maaltijden, met relatief veel bezoeken binnen één maaltijd en een hoge voeropname per bezoek, waren gerelateerd met een lage RFID en dus, met een hoge produktie-efficiëntie. Relaties tussen voeropnamepatroon en RFID werden veroorzaakt door een effect van het voeropnamepatroon op de vertering van het voer en op voeropname-aktiviteit.

In de Algemene Discussie wordt het effect van voeropnamepatroon op de voederbenutting via vertering en aktiviteitsniveau gekwantificeerd. Energetisch had het voeropnamepatroon een sterker effect via voeropname-aktiviteit dan via vertering van het voer.

Genetische aspecten van het voeropnamepatroon

In Hoofdstuk 5 wordt aangetoond, dat er lage tot gemiddelde erfelijkheidsgraden bestaan voor kenmerken van het voeropnamepatroon. De erfelijkheidsgraden waren het hoogst voor kenmerken die frequentie van eten en maaltijdgrootte beschrijven. Er werd een significant raseffect gevonden voor voeropnamepatroon en voor produktiekenmerken. NL varkens hadden minder bezoeken en maaltijden per dag en een hogere voeropname en voeropnametijd per bezoek en per maaltijd dan GY varkens. GY varkens hadden een hogere voeropnamesnelheid en een lagere voeropnametijd per dag dan NL varkens, met relatief meer grote maaltijden.

Dagelijkse groei en vleespercentage waren hoger voor GY dan NL varkens. Waarschijnlijk was dit te wijten aan een hogere maximale eiwitaanzet en lagere onderhoudsbehoefte per kg metabolisch gewicht voor de GY varkens.

In de Algemene Discussie worden gevolgen van individuele voeropnameregistraties op praktische fokprogramma's doorgerekend. Wanneer individuele voeropname (in groepshuisvesting) wordt opgenomen in de selectie-index, samen met dagelijkse groei en rugspekdikte, zal de genetische vooruitgang 20 tot 36% toenemen. Wordt dagelijkse voeropname vervangen door aantal bezoeken per dag en dagelijkse voeropnametijd, dan wordt de genetische vooruitgang 11 tot 15% hoger.

Belangrijkste conclusies

- Huisvestingssyteem heeft een significante invloed op het voeropnamepatroon, waarschijnlijk doordat er sociale interacties tussen hokgenoten optreden. Varkens in groepshuisvesting hadden grotere maaltijden, een hogere voeropnamesnelheid, minder voeropnametijd en maaltijden per dag dan individueel gehuisveste varkens. Dagelijkse voeropname werd niet significant beïnvloed door het huisvestingssysteem.
- Huisvestingssyteem heeft een significante invloed op verteringscoëfficiënten, dagelijkse groei en rugspekdikte. In individuele huisvesting waren verteringscoëfficiënten voor droge stof, rugspekdikte en groei significant hoger dan in groepshuisvesting.
- Er zijn redenen om aan te nemen dat genotype x huisvestingssyteem interacties bestaan, maar in de literatuur werd nauwelijks bewijs voor GxH interacties gevonden.
- Voeropnamesnelheid en maaltijdgrootte zijn significant positief gerelateerd met dagelijkse groei en rugspekdikte en negatief gerelateerd met vleespercentage.
- Dagelijkse voeropnametijd en frequentie van eten zijn significant negatief gerelateerd met produktie efficiëntie, door een effect op voeropname-aktiviteit en vertering. Energetisch heeft het voeropnamepatroon meer effect via voeropname-aktiviteit dan via vertering van het voer.
- Voeropname kenmerken hebben lage tot gemiddelde erfelijkheidsgraden. De hoogste erfelijkheidsgraden zijn gevonden voor kenmerken die frequentie van voeropname en maaltijdgrootte weergeven.
- Ras had een significante invloed op voeropnamepatroon en aktiviteitsniveau en, daardoor, op onderhoudsbehoefte per kg metabolisch gewicht.
- Groeps-geteste varkens kunnen geselecteerd worden met een index waarin groei en rugspekdikte zijn opgenomen. Wanneer individuele voeropname wordt opgenomen in deze selectie-index, zal de genetische vooruitgang 20 tot 36% hoger zijn. Als in

plaats van de dagelijkse voeropname het aantal bezoeken per dag en dagelijkse voeropnametijd opgenomen worden in de selectie-index, wordt de genetische vooruitgang 11 tot 15% hoger. Deze resultaten gelden alleen, wanneer alle genotypen in groepen getest worden en van alle varkens voeropname kenmerken geregistreerd worden.

- Het testen van toekomstige fokdieren in groepshuisvesting is goedkoper en de omstandigheden zijn beter vergelijkbaar met de praktijk. Wanneer de individuele voeropname niet wordt gemeten, zal de genetische vooruitgang lager zijn. In plaats van individuele voeropname kunnen dagelijkse voeropnametijd en aantal bezoeken per dag opgenomen worden in de selectie-index, hoewel de genetische vooruitgang dan iets minder groot wordt.

CURRICULUM VITAE

Lydia Cornelia Maria de Haer werd op 25 november 1962 geboren in Rotterdam. Na het behalen van het diploma Atheneum-B aan het St.-Laurenscollege te Rotterdam, begon zij in 1981 met de studie Zoötechniek aan de toenmalige Landbouwhogeschool te Wageningen. In september 1987 sloot zij de studie Zoötechniek af, met als hoofdvakken Veeteelt en Gezondheids- en Ziekteleer der Landbouwhuisdieren en als bijvak Agrarische Bedrijfseconomie.

Vanaf oktober 1987 was zij werkzaam als wetenschappelijk onderzoeker bij het Instituut voor Veeteeltkundig Onderzoek (IVO-DLO)-'Schoonoord' in Zeist. Bij dit instituut werd het onderzoek voor dit proefschrift uitgevoerd. Vanaf 15 januari 1992 is zij werkzaam als research medewerkster bij V.O.C. Nieuw-Dalland B.V.