Breeding for feed intake capacity in pigs

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Breeding for feed intake capacity in pigs

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Abstract

By selection, pig breeding organizations try to achieve genetic improvement in production and reproduction efficiency. Future genetic improvement may become constrained by a limited feed intake capacity of both growing pigs and lactating sows. In this thesis the actual feed intake capacity of growing pigs and lactating sows in relation to their potential for production and reproduction is studied. From experiments, it is concluded that feed capacity should be increased by selection during both the growth period and during lactation. The use of computerized feeding stations for recording ad libitum feed intake of growing pigs is also evaluated. Using computerized methods for data editing will increase the efficiency of the use of stations and reduce costs of feed intake recording. For pig breeding organizations, it seems justified to invest in feeding stations in order to monitor feed intake capacity of growing pigs.

Stellingen

1. Voor het betrouwbaar schatten van de gemiddelde dagelijkse voeropname gedurende de groeiperiode van een varken is het voldoende om eens per drie dagen de voeropname te meten.
Dit proefschrift

2. Voerstations kunnen efficiënter worden benut door gebruik te maken van geautomatiseerde methoden bij het controleren en verwerken van verzamelde gegevens.
Dit proefschrift

3. Met het stijgen van het aantal biggen per worp dient selectie in zeugenlijnen gericht te worden op dieren met voldoende lichaamsvet.
Knap en Luiting (1999) Paper presented at the 50th annual meeting EAAP
Dit proefschrift

4. Optimale selectie binnen zeugenlijnen leidt tot een stijging van de voeropname van vleesvarkens.
Dit proefschrift

5. Toekomstige vooruitgang in reproductieresultaten in de zeugenhouderij zal in grotere mate dan voorheen afhangen van het gedrag van de zeug en haar biggen alsmede van het omgaan daarmee door de boer.
Brooks and Burke (1998) The lactating sow. pp 301-338

6. Het huisvesten van dragende zeugen in groepen zonder dat de voeropname gestuurd kan worden leidt alleen tot welzijn op de korte termijn.

7. Wetenschappers zijn geneigd een vraag niet aan de orde te stellen voordat ze een vaag idee van een antwoord hebben.
Medawar (1955) The imperfections of man

8. Het is verbazingwekkend dat een dichtbevolkt land als Nederland tot op heden internationaal heeft kunnen concurreren op kostprijs van agrarische producten.

9. Het rapport 'Mythen & Sagen rond de varkenshouderij' is een voorbeeld van innovatief denken dat niet geremd is door de gangbare praktijk.

10. Veel conflicten in de wereld vinden hun oorsprong in de onverenigbaarheid van staatsgrenzen en culturele grenzen.

11. Echte vrienden verkiezen een feest boven een voetbalwedstrijd.

Stellingen behorend bij het proefschrift van Jaco Eissen
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Contents

1 Introduction

The overall objective of pig breeding organizations is to breed animals that produce quality lean pork at low costs and in a manner that is acceptable for society (Webb, 1997). The overall objective can be split into two components: an efficient piglet production (reproduction performance) and an efficient pork production (production performance). These two goals can be achieved by using the concept of specialized sire and dam lines according to Smith (1964). In sire lines, selection is mainly for production performance, whereas selection in dam lines is for production as well as for reproduction performance. The amount of feed eaten by growing pigs and reproducing sows is related to both production and reproduction performance. Actual feed intake is determined by the pig producer (restricted feeding) or by the ad libitum feed intake capacity of the animal. During the growing period as well as during lactation, ad libitum or semi ad libitum feeding is often applied under commercial conditions. In these phases of life, the feed intake capacity is important for production and reproduction performance, respectively.

The feed intake capacity of growing pigs is generally considered as a trait with an economic optimum. The economic optimum is usually closely related to the lowest feed conversion ratio and the lowest manure production per kg of pork (Kanis, 1995). The optimum occurs at the level where savings in total maintenance requirements through faster growth are offset by cost of increased fat deposition (Webb, 1989). During the last decades, selection in growing pigs has mainly been aimed at a combination of daily gain, feed efficiency, and carcass composition. This has improved the efficiency of pork production considerably, mainly by reductions in carcass fat (e.g., Kennedy et al., 1996). Breeding programs putting a high emphasis on feed efficiency and leanness, rather than on lean growth, reduce the appetite of growing pigs (e.g., Smith et al., 1991). As a result of genetic and non-genetic changes over the last decades, current levels of ad libitum feed intake of rapidly growing lean genotypes may be a limiting factor for realizing the maximum lean deposition capacity during at least a part of the growing period. Furthermore, many lines of pigs are now approaching optimum body fat levels with respect to meat quality (e.g., Knap and Luiting, 1999). At optimum fatness levels, efficiency of pork production should be increased further by a reduction of total maintenance requirements through faster lean growth, rather than through a further reduction of fatness (Ollivier et al., 1990). This means that feed intake capacity is likely to become a limiting factor for the full expression of lean deposition capacity.

In lactating sows, a high feed intake capacity is desired in order to maintain enough body fat and body protein during lactation so the next pregnancy will not be delayed. In dam lines, selection has been for sow fertility, mainly focussing on the number of piglets weaned per sow per year, next to the selection for production traits (Knap, 1990). As a result of genetic and non-genetic changes, litter size and milk production, and consequently nutrient requirements, have increased during the last decades (Mackenzie and Revell, 1998). On the other hand, selection for lean rapidly growing modern genotypes has reduced the amount of fat in the body of, particularly, young dam line sows at parturition and weaning (Whittemore, 1996). This reduction of body fatness of young sows means that their buffer capacity has decreased. Furthermore, selection for lean growing genotypes may have reduced feed intake capacity of sows during lactation (Kerr and Cameron, 1996). The consequence of the various developments may be that future sows of dam lines are not able to ingest sufficient nutrients in order to avoid excess mobilization of body reserves during lactation. Therefore, further improvement of reproductive efficiency may become constrained by a limited feed intake capacity during lactation.

Aim and outline of this thesis

The aim of this thesis is to study the actual feed intake capacity of growing pigs and of lactating sows in relation to their potential for production and reproduction in order to get a better understanding and to develop breeding strategies for feed intake capacity in dam and sire lines. Furthermore, the use of computerized feeding stations (i.e. feeding stations that are used for the recording of feed intake of group-housed growing pigs) is evaluated in order to reduce costs of feed intake recording and to increase benefits of investing in feeding stations for breeding organizations.

The development of computerized feeding stations enabled the recording of individual feed intake of growing pigs housed in groups. However, these feeding stations do not yet function without errors (e.g., De Haer et al., 1992; Ramaekers, 1996). As a consequence, feed intake data from feeding stations are usually analyzed after 'manual' adjustment for errors, which is subjective and time consuming. Chapters 2 and 3 present methods to trace errors in feed intake data and to deal with errors after having identified them in order to improve the efficiency of using feeding stations. The course of feed intake capacity during the test period represents information additional to average daily feed intake during the test period. Genetic aspects of the course of feed intake capacity are studied in Chapter 4 to investigate the potential of this information to increase genetic gain. Chapter 5 describes the results of an experiment with growing pigs in order to elucidate the desirable direction of selection for feed intake capacity during the early, middle, and late phase of the growing period. Chapters 6 and 7 deal with feed intake capacity of lactating sows. It is investigated whether selection for a higher feed intake during lactation should be recommended on the basis of literature (Chapter 6) and on the basis of the results of an experiment (Chapter 7). Finally, the implications of these results for selection on feed intake capacity during the growth phase and during lactation are discussed in Chapter 8 for breeding programs in dam and sire lines.

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2 Algorithms for Identifying Errors in Individual Feed Intake Data of Growing Pigs in Group-Housing

The present study describes algorithms for identifying errors in feed intake data of pigs, recorded with single-space computerized feeding stations. Potential causes of errors are failed identification of pigs or an incorrect recording of feeder weight or time by the feeding station. Feed intake data of 250 pigs, divided into 30 groups, were analyzed. Data contained 385,329 records on visits of which .95% had no identification. Nine algorithms were developed to check data for errors caused by incorrect recordings. Algorithms focused on feed intake per visit, feeding rate per visit, or on the similarity of recorded feeder weights of subsequent visits. By using all nine algorithms, 6% of the visits were classified as being incorrect. The numbers of errors needs to be kept small, as it is impossible to adjust feed intake data without bias. Results indicated several instances where a feeding station functioned sub-optimally during a period of days or weeks. Frequent checking and correction of a feeding station function during recording would, therefore, reduce these errors. Expanding a feeding station's software with the editing system described herein would allow a daily check of recorded data for errors. Furthermore, frequent maintenance of feeding stations will probably reduce the number of incorrect recordings.
Keywords: Feed station monitoring, Swine feeding, Unidentified visits.

Introduction

The use of single-space computerized feeding stations for recording individual feed intake data of growing pigs in group-housing has been the subject of several studies in recent years (e.g., De Haer, 1992; Labroue et al., 1994; Nielsen, 1995; Ramaekers, 1996). Feeding stations may be used for monitoring or controlling feed intake of pigs, or as part of scientific studies (Knap, 1995). Three common feed intake traits are feed intake, number of visits, and total visiting time per pig per day which can be used, for example, as

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selection traits in pig breeding programs (De Haer and De Vries, 1993; Von Felde et al., 1996; Labroue et al., 1997)

The functioning of feeding stations is not error-free (Knap and Van der Steen, 1994; De Haer et al., 1992; Nielsen, 1995; Ramaekers, 1996). In the literature, feed intake data from feeding stations were analyzed after errors had been adjusted for when recording was completed. It would be useful, however, to detect errors during recording to check and correct the functioning of a feeding station. The objective of this study was to develop algorithms to monitor feeding station operation by checking recorded feed intake data frequently for errors. Errors and algorithms to trace errors in feed intake data have not been described in literature, probably because feeding station software does not indicate where most errors occur. Hence, computerized algorithms to check feed intake data for errors were developed in this study, and criteria for these algorithms to identify errors were derived.

Materials and methods

Equipment and recorded data per visit

Data on individual feed intake recorded by IVOG®-feeding stations (Insentec, Marknesse, The Netherlands) were studied. The feeding station consists of an unprotected single space feeder (containing a trough), a load cell to weigh the feeder, a reservoir above the feeder, and two antennas (De Haer et al., 1992). Each pig carries an ear transponder that is activated when it is recognized by the antennas. The entrance to the feeder is adjustable in height and width to prevent two pigs from occupying the station at the same time. Weighing of the feeder is continuous with an accuracy of ca. 10 grams within a range of 0 to 50 kg. If feeder weight drops below a preset minimum (e.g., empty feeder weight + 8 kg of feed), the feeder is automatically filled with a preset amount of feed from the reservoir. Water was supplied outside the feeding station.

A feeding station records feeder weight and time at the beginning (start weight and the time) and end (final weight and time) of each visit, together with the identification number of the animal, pen number, and date. A visit starts when the antennas recognize the transponder of a pig. A visit ends when the station stops detecting the transponder, or when the station recognizes another 'stronger' transponder. The IVOG-feeding station starts recording a visit without identification when feeder weight drops considerably within a relatively short period, and no transponder is recognized by the antennas. An unidentified visit ends when feeder weight has been constant for a period or when a transponder is recognized by the antennas (Insentec, Marknesse, The Netherlands).

After each identified or unidentified visit, feed intake of the visit is computed as start weight minus final weight and duration is computed as difference (min.sec) between start time and final time. A data file in the computer controlling the feeding station stores all visits in chronological order, including fill-ups of the feeder. After collecting data from feeding stations, an extra column per visit was added to the data file for feeding rate per visit, which is feed intake divided by duration of a visit (g / min). Table 1 shows a fictive example of data on feed intake per visit.

Table 1. Fictive example of data on feed intake per visit[a]

Visits	Animal Identity / Fill-up	Start Weight (kg)	Final Weight (kg)	Feed Intake (kg)	Start Time (h:min: sec)	Final Time (h:min: sec)	Duration (min. sec)	Feeding Rate (g / min)
1	Fill-up	8.92	9.48	-.56	17:26:01	17:26:03	.02	-
2	17330577	9.48	9.48	.00	17:26:20	17:26:32	.12	.0
3	17324881	9.48	9.24	.24	17:26:34	17:32:21	5.47	41.5
4	17324881	9.25	9.74	**-.49**	17:32:41	17:32:51	.10	-2.94
5	17341906	9.74	9.02	.72	17:33:12	17:37:19	4.07	**174.9**
6	17334418	9.02	8.54	.48	17:40:22	17:54:09	13.47	34.8
7	17334374	8.54	8.56	-.02	17:54:19	17:54:42	.23	-52.2
8	Unidentified	8.56	**8.34**	.22	17:54:43	17:57:50	3.07	70.6
9	17341906	**8.30**	7.84	.46	17:57:53	18:08:33	10.40	43.1
10	Fill-up	7.84	7.84	.00	18:08:43	18:08:43	.00	-
11	17341906	8.40	8.40	.00	18:08:45	18:08:59	.14	.0

[a] Date and pen number are the same for all visits and are, therefore, omitted. Values classified as being incorrect by the algorithms have been printed in bold type

Algorithms and criteria to identify errors

Based on literature (Knap, 1995; De Haer et al., 1992) and the authors' own experiences with feed intake recordings, errors were divided into two categories. Type A errors are unidentified visits, which can easily be traced in the data (e.g., Visit 8, Table 1). An error of type A1 can occur when a transponder is out of order or when a pig loses its transponder (De Haer et al., 1992; Knap and Van der Steen, 1994; Nielsen, 1995), error A2 can occur when two visits happen in rapid succession (Nielsen, 1995), error A3 can occur when the quality of a transponder signal is decreasing, or error A4 can occur when identification system tuning is sub-optimal. If the quality of a transponder signal is decreasing, a transponder needs to be closer to the antennas before the feeding station recognizes the identification. Errors A1 and A3 only affect pigs with a transponder problem; whereas errors A2 and A4 may affect any pig. To diagnose possible causes of failed identification, the number of unidentified visits per station per test day was studied,

Table 2. Overview of algorithms and criteria used to identify incorrect recordings of feeder weight or time (type B errors)

Algo-rithm	Feed Intake Information	Visits Involved	Criteria for Classifying Recordings as Incorrect
1	Feed intake per visit (FIV)	All	FIV < -.02 kg
2		All	FIV > 2.00 kg
3		Duration = zero seconds	Abs (FIV) > .01 kg
4	Feeding rate per visit (FRV)[a]	.00 < FIV < .05 kg (category I)	FRV > 600.00 g / min
5		FIV ≥ .05 kg, preceding or following a visit with FIV < -.02 kg (category IIa)	FRV > 110.00 g / min
6		FIV ≥ .05 kg, not preceding or following a visit with FIV < -.02 kg (category IIb)	FRV > 150.00 g / min
7		FRV = 0 g / min	Duration > 250 seconds
8		All, except for FRV = 0 g / min	Abs (FRV) ≤ 2.00 g / min
9	'Difference'[b] (DIF)	All, except visits with .40 ≤ DIF ≤ .70 kg preceded by a fill-up	Abs (DIF) > .02 kg[c]

[a] FRV was not computed for visits lasting zero seconds

[b] Difference = start weight of present visit - final weight of preceding visit

[c] Present visit and its preceding visit are classified as being incorrect

as well as feed intake and duration of unidentified visits and total daily feed intake during unidentified visits.

Type B errors are caused by incorrect recordings of feeder weight or time, and include both identified and unidentified visits. Error B1 includes an incorrect recording of start or final feeder weight, resulting in an incorrect value of feed intake of a visit. A possible cause of an incorrect feeder weight is accumulation of material under the feeder (De Haer et al., 1992; Knap and Van der Steen, 1994). Error B2 includes an incorrect recording caused by software that controls functioning of a feeding station. A B2 error may occur, for example, when a feeding station cannot record the feeder weight correctly because two visits occur in rapid succession. Final weight of the first visit and start weight of the second have to be generated according to software procedures. Error B3 originates from a pig that is identified by the feeding station while in proximity, but not eating (Von Felde, 1996). B3 errors may be caused by a sub-optimal tuning of the identification system.

Algorithms and criteria were developed to identify type B errors in the data (Table 2), as these errors were not indicated by the software of a feeding station. Algorithms focused on feed intake per visit, feeding rate per visit, or on similarity of feeder weight recordings of subsequent visits. Some of the criteria were derived as a result of the analysis. Therefore, justification of algorithms and criteria is presented in the results section.

Feed intake data

Individual data on ad-libitum feed intake of 250 growing pigs were used for this study. Data were recorded by IVOG-feeding stations at three breeding herds of Stamboek and Dumeco Breeding. Pigs were tested in groups of 6 to 12 per pen, for a variable period with a maximum of 110 days (on average 91 days). Data contained 385,329 records on visits of which 3,659 were unidentified (.95%). There were 105,511 records on filling up the feeder. At herd 1, six feeding stations were used during one test period (groups 1.1 to 6.1 which signify number of feeding station.test period). At herd 2 and 3, six feeding stations were used during two successive test periods (groups 7.1/7.2 to 12.1/12.2 for herd 2 and groups 13.1/13.2 to 18.1/18.2 for herd 3). Results are presented per group in Figures 3 and 6. In total, 30 groups were tested with 18 feeding stations during 2,714 test days.

Results

Unidentified visits

Feed intake per unidentified visit ranged from -1.27 to 9.11 kg, and duration of unidentified visits ranged from zero seconds to more than 22 min. More than 82% of unidentified visits had a feed intake ≤ .05 kg; whereas only 45% of all visits had a feed

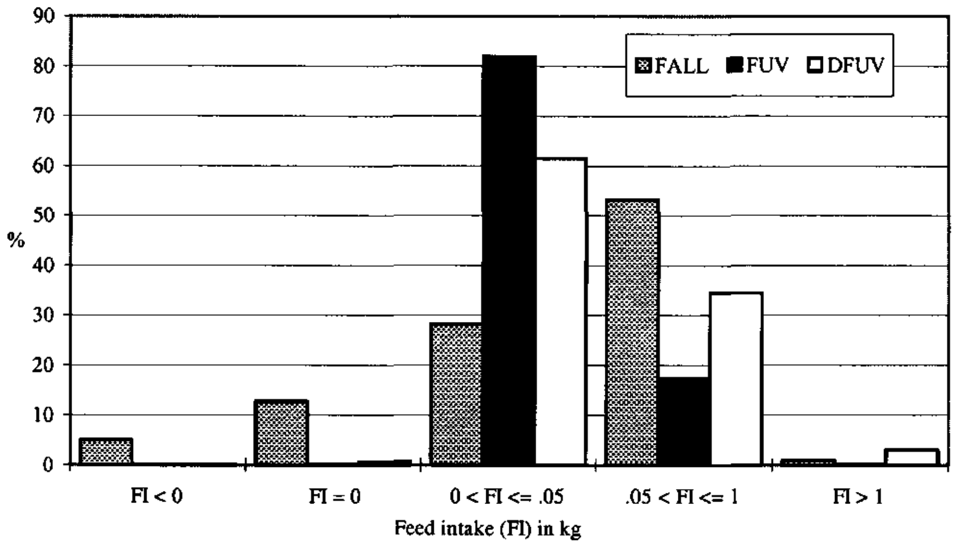

Figure 1. Distribution of feed intake per visit of all visits (FALL; N = 385,329) and of unidentified visits (FUV; N = 3,659), and total daily feed intake during unidentified visits (DFUV) per station of test days with at least one unidentified visit (N = 1,280).

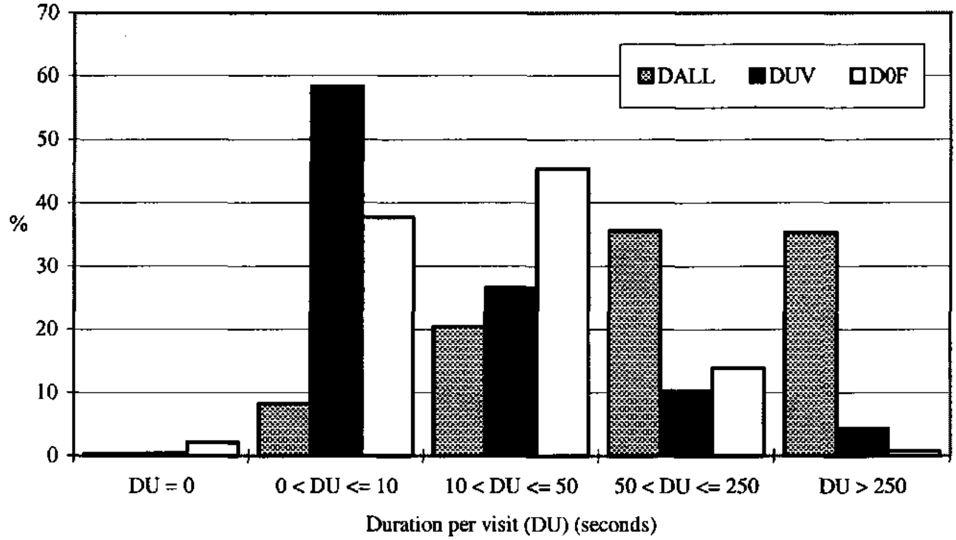

Figure 2. Distribution of duration per visit of all visits (DALL; N = 385,329), of unidentified visits (DUV; N = 3,659), and of visits with feed intake equal to zero kg (D0F; N = 48,732).

intake ≤ .05 kg (Figure 1). Furthermore, 85% of unidentified visits lasted ≤ 50 s; whereas, only 29% of all visits lasted ≤ 50 s (Figure 2).

Of the 2,714 test days, 52.8% had zero unidentified visits, 34.0% had 0 < unidentified visits ≤ 2, and 9.1% had 2 < unidentified visits ≤ 5. A proportion of .4% of test days had more than 25 unidentified visits, up to a maximum of 44. Figure 1 shows the distribution of total daily feed intake during unidentified visits of all test days with ≥ 1 unidentified visits. A proportion of 62% of these test days had a total daily feed intake ≤ .05 kg.

Groups 2.1 and 11.2 had more unidentified visits than other groups (Figure 3). Both groups had a period of 20 test days with > 19 unidentified visits per day (on average) and a total daily feed intake during unidentified visits > .6 kg. As each transponder was recognized daily during these periods, loss of a transponder (error A1) was not the cause of these results.

Justification of algorithms and criteria for identifying incorrect measurements of feeder weight or time

In total, nine algorithms were developed as summarized in Table 2. The number of visits classified as being incorrect are presented per algorithm in Table 4. The first three algorithms focused on feed intake per visit, which ranged from -9.23 kg up to 19.98 kg.

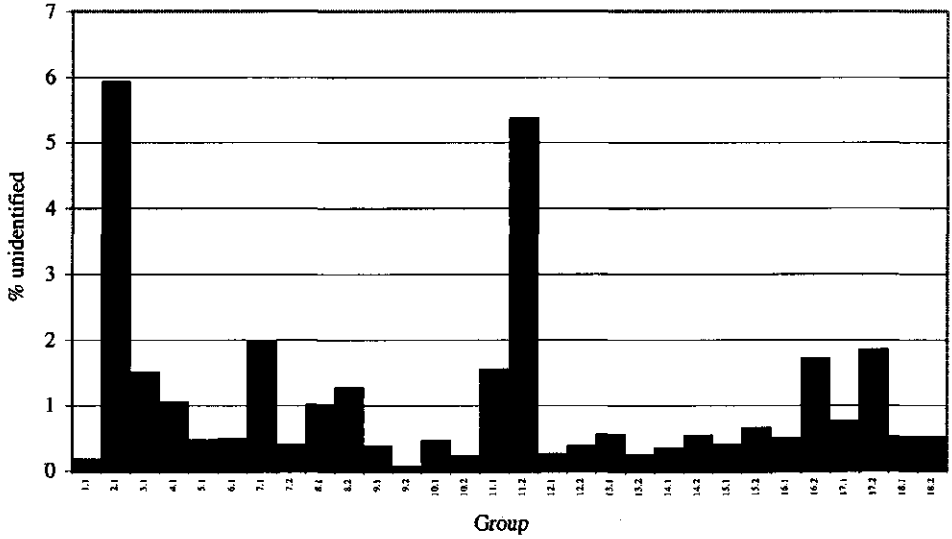

Figure 3. Proportion of unidentified visits per group.

An incorrect value for feed intake per visit is caused by an incorrect recording of start or final feeder weight. Algorithm 1 focused on visits with a negative value for feed intake. A negative value means that final feeder weight was larger than start feeder weight. A small increase in feeder weight during a visit may be the result of, for example, an amount of saliva falling from a pig's mouth into the feeder's trough. If no feed is eaten during such a visit, the result will be a negative value for feed intake. Furthermore, a small change in feeder weight may cause a change in recorded feeder weight of 10 grams due to rounding. Negative values of feed intake per visit of -.02 and -.01 kg, therefore, were tolerated (e.g., Visit 7, Table 1); whereas values < -.02 kg were arbitrarily classified as being incorrect (e.g., Visit 4, Table 1).

Algorithm 2 focused on large values for feed intake per visit. Based on the analysis, it was decided to classify visits with a feed intake > 2 kg as being incorrect. Algorithm 3 focused on visits lasting zero seconds. In the data, values found for feed intake ranged from -.52 to .93 kg. Feed intake of such a visit is expected to be zero kg. Intake data, however, may deviate slightly from zero due to a small change in feeder weight, combined with rounding. Therefore, visits lasting zero seconds were only classified as being incorrect if the absolute value for feed intake was > .01 kg.

Algorithms 4-8 focused on feeding rate per visit (FRV) of visits lasting ≥ 1 s. Algorithms 4-6 checked for large values for FRV caused by an incorrect recording of start or final feeder weight. Calculating the FRV as feed intake divided by duration of a visit

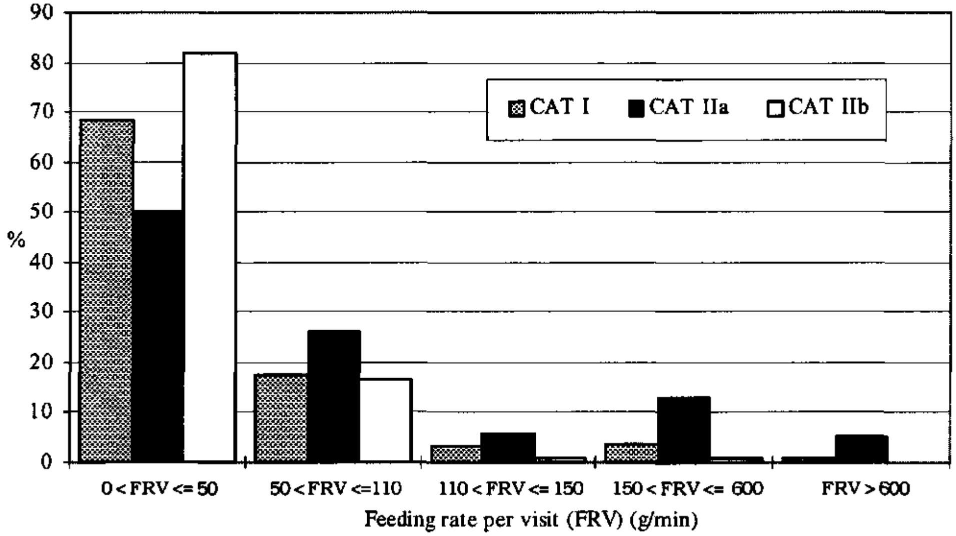

Figure 4. Distribution of feeding rate per visit of visits lasting at least one second with 0 < feed intake (FIV) < .05 kg (CAT I; N = 95,757), with FIV ≥ .05 kg and preceding or following a visit with FIV < -.02 (CAT IIa; N = 7,728), and all other visits with FIV ≥ .05 kg (CAT IIb; N = 213,496).

introduces a high level of variation. Short visits often result in a large FRV value when a mouthful of feed is taken from the feeder (Nielsen, 1995). Therefore, two categories of visits were distinguished: (I) 0 kg < feed intake < .05 kg (algorithm 4); and (II) feed intake ≥ .05 kg. Within category II, visits were divided over two sub categories: IIa, visits directly preceding or following a visit with a feed intake < -.02 kg (algorithm 5), and IIb, all other visits (algorithm 6). Visits with a negative value for feed intake were often directly preceded or followed by a visit with an elevated positive feed intake value (e.g., Visits 4 and 5, Table 1). Category IIa visits were, therefore, subjected to more stringent criteria for FRV than category IIb visits. Figure 4 shows the distribution of FRV of category I, IIa and IIb visits. Criteria were arbitrarily set to FRV > 600 (algorithm 4), FRV > 110 (algorithm 5), and FRV > 150 g / min (algorithm 6).

Algorithms 7 and 8 checked for small absolute values for FRV of visits, caused by an incorrect recording of start or final feeder weight or time (error B3). Visits with FRV equal to zero g / min, that lasted more than 250 s (DOF, Figure 2) were arbitrarily classified as being incorrect (algorithm 7). Visits with an absolute value 0 < FRV ≤ 2 g / min were also classified as being incorrect (algorithm 8).

Table 3. Distribution of 'difference' between start weight of present visit and final weight of preceding visit (N = 385,329)

'Difference'[a] (DIF) (kg)	Percentage
< -.02	1.1
-.02 ≤ DIF < 0	10.5
0	78.2
0 < DIF ≤ .02	7.9
.02 < DIF < .40	.4
.40 ≤ DIF ≤ .70	1.9
> .70	.0
No value[b]	.0

[a] Difference = start weight of present visit - final weight of preceding visit

[b] Values for difference could not be computed for each first visit on test day 1 per group, and for each visit directly following technical operations of stations

.0 One or more records

Algorithm 9 examined the connection between subsequent visits by calculating 'difference', which is defined as start weight of one visit minus final weight of the preceding visit (Table 3). Values found for difference varied from –30.27 to 19.98 kg. Assuming there were no environmental effects on feeder weight, difference should equal 0. Because conditions may change slightly between visits, small absolute values for difference up to .02 kg were tolerated (e.g., Visits 3 and 4, Table 1). If a feeding station fails to record final feeder weight of a fill-up before a pig is identified, then final weight is set equal to the start weight of the fill-up. Start weight of the visit, subsequently, is computed as start weight of the fill-up plus average size (kg) of the last ten undisturbed fill-ups (e.g., Visit 11, Table 1; Knap and Van der Steen, 1994). In the data, close to 99% of all fill-up sizes differing from zero kg varied from .40 to .70 kg. Visits with .40 ≤ difference ≤ .70 kg, preceded by a fill-up with equal start and final feeder weights, therefore, were also considered to be correct. In all other cases, however, both the present and its preceding visit were classified as being incorrect because it was generally not clear whether start weight of the present visit or final weight of the preceding visit was incorrect (e.g., Visits 8 and 9, Table 1).

Applying the criteria of all nine algorithms resulted in 23,217 visits classified as being incorrect, or 6.0% of all visits. Some visits were incorrect due to more than one algorithm. The overlap, as indicated in Table 4, was caused largely by algorithms 1 and 9. Algorithm 2 also indicates pronounced overlap with algorithms 5 and 6. The table indicates that 90% of visits (62.2 + 27.8) with feed intake greater that 2 kg also had high feeding rates.

Table 4. Number (N) of unidentified visits (UV) and visits classified as being incorrect per algorithm[a], and their degree of overlap as % of N

Algorithm	UV	1	2	3	4	5	6	7	8	9
UV		0.0	4.4	9.5	76.1	8.7	9.1	-	-	6.7
1	0.1		-	15.2	-	-	-	-	1.1	18.6
2	0.1	-		-	-	3.0	1.3	-	-	0.3
3	0.3	0.2	-		-	-	-	-	-	0.1
4	16.2	-	-	-		-	-	-	-	2.7
5	4.4	-	62.2	-	-		-	-	-	2.3
6	5.4	-	27.8	-	-	-		-	-	1.6
7	-	-	-	-	-	-	-		-	0.3
8	-	0.0	-	-	-	-	-	-		0.4
9	22.6	26.6	41.1	16.2	42.2	15.0	9.3	8.6	15.6	
N	3,659	8,587	90	105	777	1,858	2,155	384	276	12,259

[a] See Table 2 for algorithms numbers

.0 One or more records

Large differences were found between groups concerning proportion of incorrect visits (Figure 5). Table 5 presents the distribution of incorrect visits per algorithm for each group with at least 10% visits classified as being incorrect. Each of these groups had a period of at least two weeks with a relatively large proportion of incorrect visits, indicating that the feeding station was functioning sub-optimally during this period. In each case either algorithm 1 or 9 was the main cause of the large proportion of incorrect visits.

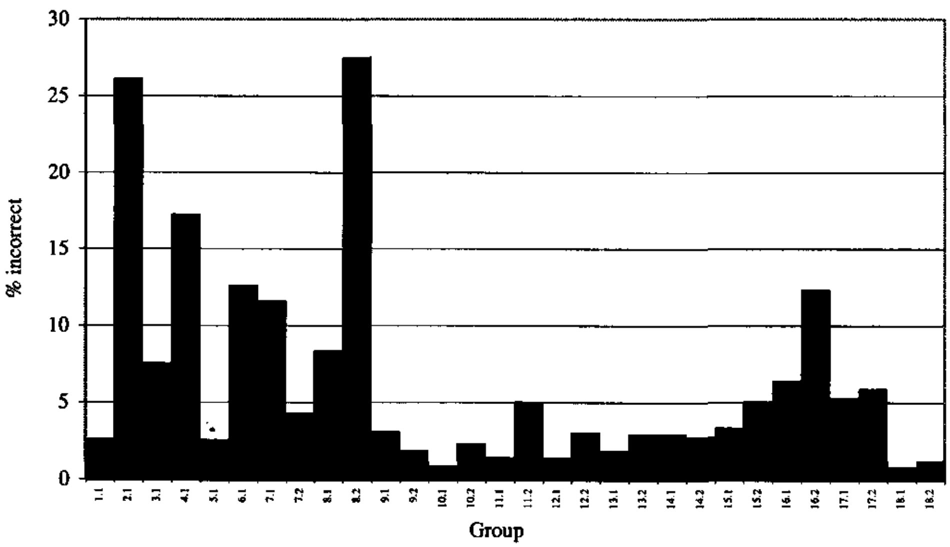

Figure 5. Proportion of visits classified as being incorrect per group.

Table 5. Proportion of visits classified as being incorrect per group (total), and per algorithm[a] for groups[b] with more than ten percent visits classified as being incorrect

		Algorithm								
Group	Total	1	2	3	4	5	6	7	8	9
2.1	26.0	11.2	.0	.0	1.6	2.1	1.4	.0	.1	19.0
4.1	17.2	9.0	-	-	.3	1.4	2.0	.3	.3	4.8
6.1	12.5	4.0	-	.0	.1	.6	2.0	.0	.1	7.2
7.1	11.6	4.8	.2	.0	.2	.7	.4	.2	.1	10.1
8.2	27.4	14.3	.3	.0	.3	6.0	3.0	.3	.2	5.7
16.2	12.2	3.8	-	.2	.3	.6	1.8	.2	.1	6.0

[a] See Table 2 for algorithms numbers

[b] See text

.0 One or more records

Twelve feeding stations were used during two subsequent test periods (groups 7.1 / 7.2 to 18.1 / 18.2 which signify number of feeding station.test period). Nine of these stations showed a higher percentage of incorrect visits during the second test period than during the first test period (Figure 5). Using a feeding station for a longer period without maintenance seems to increase the number of errors. These errors most likely involve incorrect recording of start or final feeder weights (B1 errors). Additionally, these errors may have been the main cause of the somewhat larger proportion of incorrect visits per test day during the second part of the test period than during the first part of the test period (Figure 6).

Relationship between unidentified visits and visits classified as being incorrect

In total, 5.9% of visits classified as being incorrect were unidentified. Algorithm 4 and 9 were the main factors, respectively classifying 16.2 and 22.6% of unidentified visits as being incorrect (Table 4). Visits classified as being incorrect because of algorithm 4 were for 76.1% unidentified (Table 4).

Herd

Proportions of unidentified and incorrect visits are presented per group in Figures 3 and 6, respectively. At herd 1 (groups 1.1 to 6.1), 1.47% of the visits were unidentified and 11.8% were classified as being incorrect; at herd 2 (groups 7.1 to 12.2), .97% of the visits were unidentified and 5.8% were classified as being incorrect; at herd 3 (groups 13.1 to 18.2), .69% of the visits were unidentified and 3.9% were classified as being incorrect. Possible causes for differences may be the differing states of station

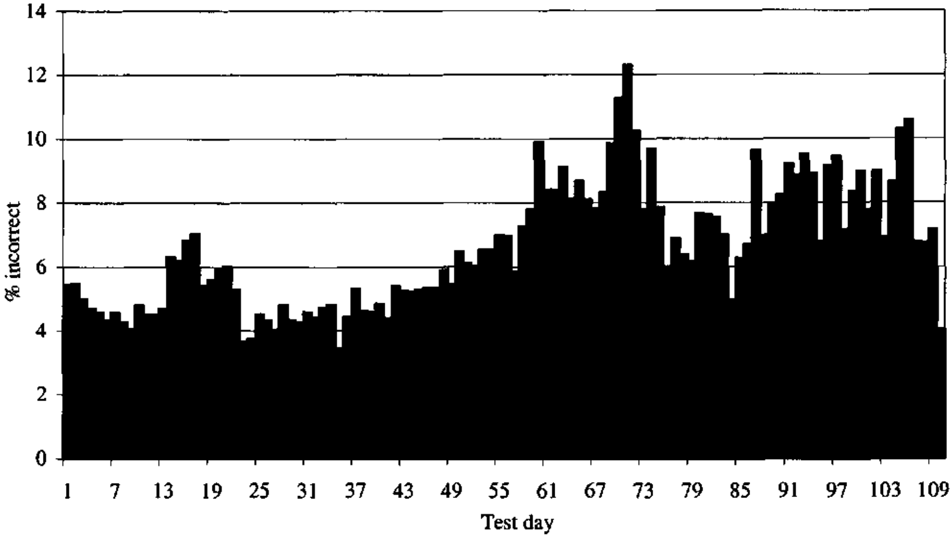

Figure 6. Proportion of visits classified as being incorrect per test day.

maintenance, number of pigs per pen, sex and genotype of pigs tested, or extent of a farmer's experience in working with feeding station.

Summary and discussion

Data on ad-libitum feed intake were studied for errors to develop algorithms for monitoring feeding station function. Errors were divided into two categories: Unidentified visits (type A errors) and incorrect recordings of feeder weight or time (type B errors). Potential causes for type A errors are loss of transponder (A1), rapid succession of two visits (A2), decrease in transponder signal quality (A3), or sub-optimal tuning of the identification system (A4). Potential causes for type B errors are recording of an incorrect start or final feeder weight of a visit (B1), incorrect recording caused by controlling software (B2), or identification of non-visiting pigs (B3).

Unidentified visits

Type A1 errors were the only errors that could be distinguished from other type A errors. During a period of several days one of the transponders in a pen was not identified while the number of unidentified visits was elevated to 5 to 20 per day. The total daily feed intake during unidentified visits ranged from .5 to 3 kg. A proportion of these unidentified visits, however, may have been caused by type A2-A4 errors.

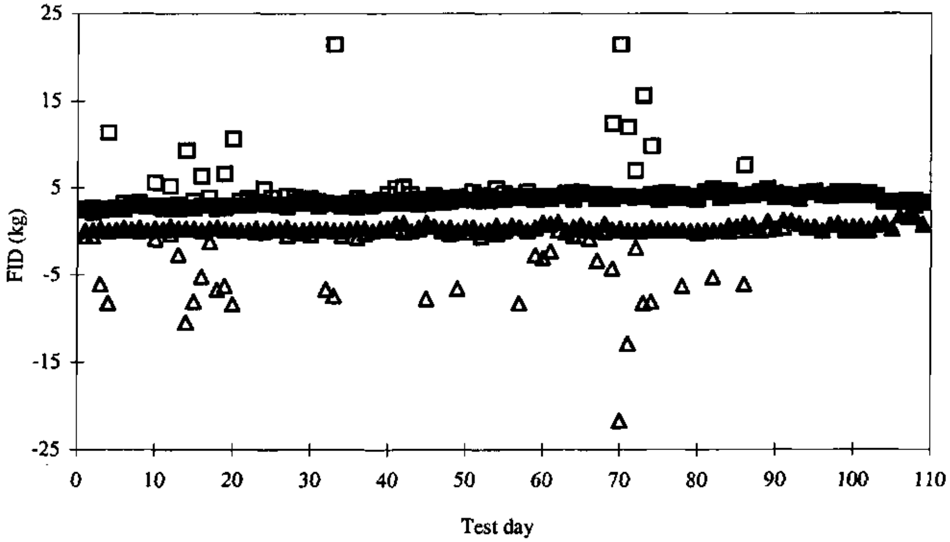

Figure 7. Minimum and maximum values for feed intake per day (FID) per pig per test day before (△, □) and after (▲, ■) eliminating visits classified as being incorrect.

Errors A2-A4 were probably the most important causes of failed identification. This is supported by relatively large proportions of unidentified visits with a short duration or small feed intake and by the large proportion of test days with a small value for total daily feed intake during unidentified visits. Moreover, the large number of unidentified visits in groups 2.1 and 11.2 were not caused by A1 errors.

Algorithms and criteria for identifying incorrect measurements of feeder weight or time

Each criterion used to judge the correctness of a feed intake recording was subjective. Therefore, some visits may have been falsely assumed to be correct or incorrect. Figure 7 shows the minimum and maximum values found for feed intake per day (FID) per pig per test day before and after eliminating visits classified as being incorrect. To calculate FID records only identified visits were used. Before elimination, the analysis included 27,741 records on FID. After elimination, only 18,142 records were left, because FID was computed only when none of a pig's visits on a test day was classified as being incorrect. Figure 7 shows that all outlying values for FID disappeared after elimination, indicating that all large errors were identified. It may, therefore, be concluded that the presented combination of algorithms can be used to check the function of a feeding station.

Relationship between unidentified visits and visits classified as being incorrect

The way unidentified visits are generated indicates that these visits will more often last a shorter period than identified visits. Unidentified visits, therefore, will more often have a large value for FRV or a duration of zero seconds, and less often a small value for FRV. Consequently, algorithms checking visits of zero seconds and visits with large FRV values (algorithms 3 to 6) showed a relatively strong overlap with unidentified visits; whereas, visits being incorrect because of small FRV values (algorithms 7 and 8) were all identified (Table 4). Since feeding stations only start recording unidentified visits when feeder weight drops, algorithm 1 hardly classified unidentified visits as being incorrect.

Optimal tuning of the identification system is important to assure proper functioning of the feeding station. A sub-optimal tuning in one direction may increase the number of unidentified visits; whereas, the number of B3 errors may increase when tuning is sub-optimal in another direction.

Type of feeding station

Station type may affect proportion of visits without identification, criteria of algorithms, and the number and relative importance of different types of errors. Various types of feeding stations differ in the design of entrance, in level of protection to the visiting pig (Nielsen et al., 1995), and in controlling software procedures. In this study only IVOG-feeding stations were used.

Concluding remarks

Visits without identification, and incorrect measurements of feeder weight or time at the beginning or end of a visit were the two types of errors on which this study focused. Feed intake data of unidentified visits cannot easily be allocated to pigs because it was generally not clear which pigs caused unidentified visits. It would be difficult to adjust visits classified as being incorrect because it was not apparent what the true data should be. Moreover, causes of incorrect visits can vary, making it impossible to use standard solutions for adjusting data. Therefore, the number of unidentified visits and visits classified as being incorrect need to be kept small (Knap and Van der Steen, 1994).

Results indicated several instances where a feeding station did not function optimally during a period of days or weeks. Frequently checking recorded data and correcting the feeding station's function will, therefore, reduce numbers of errors. This study showed that by checking for the occurrence of unidentified visits and for incorrect feed intake recordings by using nine algorithms, function of a feeding station can be successfully monitored. Expanding a feeding station's software with the editing system described herein would allow a daily check of recorded data for errors. Furthermore, frequent maintenance of feeding stations (e.g., between test periods) may reduce the number of visits classified as being incorrect.

Control routines could be further extended to frequently check the accuracy of a feeding station's recording of weight. A possible routine could add a pre-weighed amount of feed to the feeder and check the recorded value. At present, identification and adjustment of errors is a subjective process (e.g., De Haer et al., 1992; Von Felde, 1996). The presented editing system provides a more systematic method of identifying errors in feed intake data for growing pigs in group housing.

Acknowledgments

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3 Effect of Missing Data on the Estimate of Average Daily Feed Intake of Growing Pigs

The effect of missing records for feed intake per day (FID) on the estimate of average daily feed intake (DFI) during the test period of individual pigs was studied. Data from 192 growing pigs tested with single-space computerized feeding stations during an average of 93 d were used. True DFI was computed by averaging FID records per pig, individually. A first and third degree polynomial, and a nonlinear function were fit to FID records per pig to estimate DFI by averaging estimated FID records per pig, individually. The three functions showed small differences for goodness of fit. The missing of FID records was simulated by random as well as period wise deletions of FID records. The effect of missing FID records was judged on the Pearson correlation between true and estimated DFI. Deleting randomly up to 70% of FID records per pig before fitting each function reduced this correlation only from 1.00 to .96 for each function. Deleting 25 successive FID records (about 27% of records) before fitting reduced the correlation to values ranging from .92 to .96 and from .59 to .96 for the first and third order degree polynomial function, respectively, and from .80 to .97 for the nonlinear function. Using iteratively reweighted least squares regression methods to exclude undesirable effects of outlier values gave similar results for the effect of missing FID records on estimated DFI. Results imply that considering incorrect FID records as missing is a good alternative for adjusting incorrect data in combination with using functions to estimate DFI of growing pigs. Use of a first degree polynomial function is recommended. Moreover, use of functions enables a more efficient use of feeding stations by recording feed intake data during only parts of the test period.

Key Words: Growing pigs, Feed intake curves, Missing data, Feeding stations

Introduction

Average daily feed intake (DFI) during the test period of breeding pigs is usually utilized in pig breeding programs because of its economic importance (e.g., Krieter, 1986;

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Eissen, J.J., A.G. de Haan, and E. Kanis. 1999. Effect of missing data on the estimate of average daily feed intake of growing pigs. Journal of Animal Science 77:1372-1378.

Kanis, 1988). Nowadays, many breeding organizations are using computerized feeding stations for the recording individual feed intake data of pigs in group housing. Primary reasons for testing pigs in groups are lower costs of housing per test place and avoidance of possible genotype by housing system interactions (De Haer and Merks, 1992). Recorded data on feed intake per visit to the feeder are usually summarized per pig to feed intake per day records (FID).

The functioning of computerized feeding stations is not always without error (De Haer et al., 1992; Knap and Van der Steen, 1994; Nielsen, 1995; Ramaekers, 1996). Recorded data, therefore, are often analyzed after adjustments for errors. In literature, incorrect data are usually adjusted per visit (e.g., De Haer et al., 1992). Instead of adjusting, which is time consuming and subjective, FID records containing incorrect data could be eliminated and considered as missing values (Knap, 1995). Hence, the objective of this investigation was to study the effect of missing FID records (total numbers and positions within the test period) on the estimate of DFI per pig.

Materials and methods

The basis idea was to simulate the missing of FID records according to certain strategies in feed intake data of pigs that had for each test day a correct FID record. The effect of missing FID records on the estimate of DFI will be estimated by using feed intake curves.

Data

Ad libitum feed intake data of 855 growing pigs recorded on three genotypes (Duroc, Yorkshire, and Dutch Landrace) and two sexes (boars and gilts) in three breeding herds of Stamboek and Dumeco Breeding were available. The IVOG®-feeding stations (Insentec, Marknesse, The Netherlands; De Haer et al., 1992; Eissen et al., 1998) were used for recording individual feed intake data. Pigs were tested in groups of 8 to 12 animals. The variation in number of test days was large with a minimum of 3 and a maximum of 110 d due to the experimental stage of feed intake recording at this time. Most pigs had finished their performance test and had recorded feed intake data for each test day. Some pigs, however, had not finished their test because they died or were discarded before end of test or were still under performance test at the time of data collecting.

Nine edit algorithms described by Eissen et al. (1998) were used to identify errors in recorded data caused by an incorrect recording of feeder weight or time. These algorithms focused either on feed intake per visit, feeding rate per visit, or recorded feeder weights of subsequent visits, and classified visits either as being correct or incorrect. Next, feed intakes per visit were summarized to FID records. An FID record was eliminated if one or more of a pig's visits on that particular day were classified as being incorrect. On average, 29% of individual FID records were eliminated per pig. For each pig, the first test day with a noneliminated FID record is referred to as test day 1 and the last test day with a noneliminated FID record is referred to as the last test day.

Approimately 200 pigs with recorded feed intake data were considered appropriate for this study. Four criteria were used to choose pigs for the analysis. Criterion 1): length of test period ≥ 75 d, which allowed us to study the effect of timing of missing FID records within the test period on estimate of DFI. Criterion 2): at least three of the first five test days had to have a FID record, as preliminary analyses indicated that for some procedures the first part of the test period was of major importance to estimate DFI. Criterion 3): pigs were allowed to have only once a maximum of three eliminated FID records in a row, which ensured the presence of data over the whole test period. Finally, pigs with the highest percentage of noneliminated FID records were selected as this would facilitate the analysis. Therefore, criterion 4) was set to ≥ 87% correct FID records which resulted in a data set of 192 pigs. This data set is referred to as SET1. These pigs were tested for an average of 93 d starting at an average age of 79 d, and had only 7.9 eliminated FID records (range 2-14). Eissen et al. (1998) concluded that a feeding station malfunction is the primary cause of eliminated FID records. Therefore, we believe that the use of these four criteria had not resulted in a biased sample of pigs with respect to feed intake patterns.

Data in SET1 originated from two herds. The herd that dropped out had relatively few pigs with recorded feed intake data as this herd just started using computerized feeding stations. Moreover, this herd tested pigs for a shorter period up to 90-95 kg of body weight, whereas, both other herds tested pigs up to about 110 kg. SET1 contained data of 158 boars and 34 gilts. Genotype and sex were entangled with herd. Body weight at beginning and/or end of test was not always recorded due to the experimental stage of feed intake recording. Animals with records were tested from an average of 28 kg (n=125) up to 108 kg of body weight (n=189).

Feed intake curves

First- and third-degree polynomial functions (respectively, P1 and P3) and a nonlinear function (NL) were fitted per pig to FID records (Proc NLIN, using Gauss-Newton; SAS, 1990):

$$\mathrm{EFID}(t) = a_1 + b_1 t \quad \text{(P1)}$$

$$\mathrm{EFID}(t) = a_2 + b_2 \ln(t + c_1) \quad \text{(NL)}$$

$$\mathrm{EFID}(t) = a_3 + b_3 t + c_2 t^2 + d_1 t^3 \quad \text{(P3)}$$

where EFID(t) is the estimated feed intake at test day t, a_*, b_*, c_*, and d_* are function parameters, and ln is the natural logarithm. These three functions were chosen because of an increasing flexibility from function P1 to P3, as reflected by the increasing number of parameters. Polynomial functions are commonly used for fitting feed intake data (e.g., Krieter, 1986; NRC, 1987, Kanis and Koops, 1990; Andersen and Pedersen, 1996). Moreover, the NL function was chosen because of its possibility of plateauing feed intake per day at higher numbers of test days. To guarantee convergence at a global maximum, it was necessary to bound parameters and to provide proper starting values for NL. Bounds used were $a_2 > -45$, and $c_1 > .0001$, and starting values were $a_2 = -1$, $b_2 = 1$, and $c_1 = 10$. The convergence criterion was 10^{-10}.

Temporary drops or rises in FID cause large residuals when fitting a function to individual FID records per pig. Environmental factors like an outbreak in disease (e.g., Ramaekers, 1996), vaccination, or change of diet may cause drops. For genetic analysis or for studying biological patterns of feed intake, such depressions in recorded feed intakes are usually less informative than data of other days. When using least squares regression, however, these 'outliers' have a relatively large impact on the fit of a function (Birch and Fleischer, 1984). Iteratively reweighted least squares (IRLS) regression methods protect against such undesirable effects as large residuals are weighted lower (Birch and Fleischer; 1984; Grossman and Koops, 1988). Each functions was, therefore, also fitted to the data by using IRLS (Proc NLIN, using Gauss-Newton iterative method; SAS, 1990). The statistical weight of each FID record for fitting with IRLS was e^{-u^2}, where e is the base of the natural logarithm and u is the scaled residual for that record (Holland and Welsch, 1977; Grossman and Koops, 1988). The scaled residual was obtained by dividing each residual by .42, which was the average RSD per pig fitting P3 without IRLS (Table 1). This value was used for each function as differences in RSD between functions were small. Estimated parameters per animal without IRLS were used as starting values for fitting functions with IRLS (Birch and Fleischer, 1984). For the initial iteration, the statistical weight for each FID record was unity. For each next iteration, statistical weights were determined by the reweighting procedure.

Goodness of fit

Residual standard deviation (RSD), coefficient of determination (R^2), and the Durbin-Watson (DW) statistic (Durbin and Watson, 1951), which measures the first-order autocorrelation of residuals, were calculated to judge the fit of each function. If residuals are not autocorrelated, DW should be close to 2. RSD (Grossman and Koops, 1988), R^2, and DW were computed using weighted information when IRLS was used.

Each function was used to estimate DFI with and without IRLS. EFID was only estimated for test days with a noneliminated FID record. True and estimated DFI were computed per pig by individually averaging FID and EFID records, respectively. Results were judged on the Pearson correlation between true and estimated DFI. The Pearson correlation was also computed for three 25-d periods (period 1 to 3; d 1 to 75) and the remaining period (period 4), separately, to get an indication of the fit in parts of the test period. This is referred to as the correlation between true and estimated $DFI_{(period)}$.

Estimating eliminated FID records

The best starting point to study the effect of missing FID records on estimated DFI would be a data set with a FID record for each test day. Therefore, a second data set (SET2) was generated by estimating FID records that were eliminated because of incorrect data. These records were estimated per pig using SET1 by averaging FID records of the two preceding and two following test days with a noneliminated record, with a stochastic component added to that. The stochastic component was a random number drawn from a standard normal distribution multiplied by .42, which was the average RSD per pig fitting P3 without IRLS (Table 1). If the FID record of the second or the next to last day of a pig's test period was eliminated, then the estimate was based on three instead of four days. Next, each estimate was defined as a noneliminated FID record resulting in a FID record for each pig for each test day in SET2. True DFI of SET2 was, therefore, based on information of each test day.

Effect of missing FID records on the estimate of DFI per pig

Missing FID records were simulated by deleting FID records in SET2. After deleting, each function was fitted to all nondeleted FID records per pig with and without IRLS. EFID was estimated for each deleted and nondeleted test day and DFI was estimated, subsequently. The FID records were deleted according to two alternatives. In alternative one, a proportion of 10 to 90% of an animal's FID records was randomly deleted with steps of 10% to simulate random missing values. Alternative two simulated a complete malfunctioning of a feeding station during a period of several weeks by deleting FID records in periods. Accordingly, all FID records in period 1 to 4 were deleted separately, but also in combinations of two periods. Results were judged on the Pearson correlation between true DFI and estimated DFI, based on nondeleted FID records.

Results

Some pigs had a similar fit for each function, whereas others showed differences. An example of the latter is in Figure 1. For some pigs, IRLS did not, or only slightly, affect the fit, whereas, for others effects were considerable. The correlation between true $DFI_{(SET1)}$ and true $DFI_{(SET2)}$ was .99.

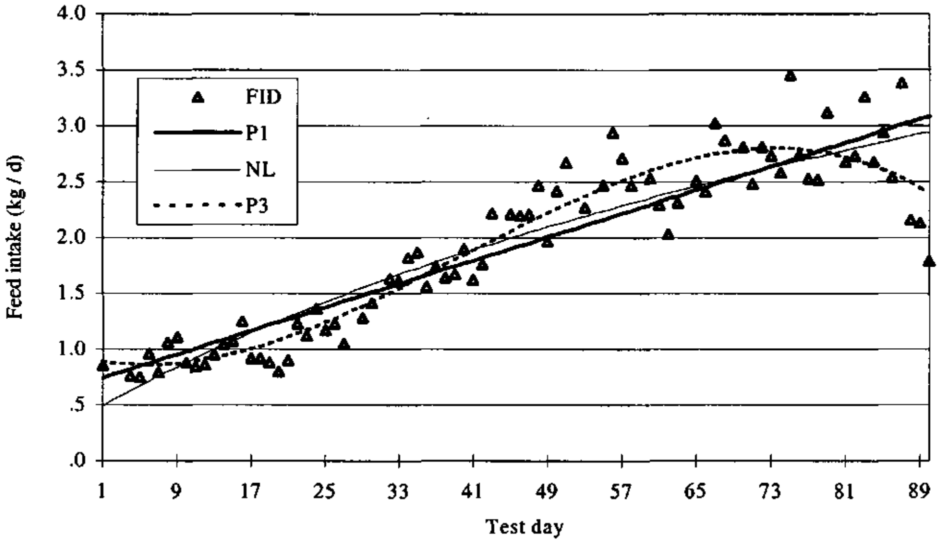

Figure 1. True (FID) and estimated records on feed intake per day (kg) using a first (P1) or third (P3) degree polynomial, or a nonlinear (NL) function plotted against test day for one pig.

Goodness of fit (SET1)

Results for goodness of fit were best for P3 (Table 1), however, differences between functions were small, both for fitting with and without IRLS. As a consequence of using weighted information, fitting with IRLS improved results for RSD, R^2 and DW. Each function had a mean DW < 2, indicating a tendency to a positive correlation among residuals of subsequent FID records. In total, 55.2, 47.9, and 37.0% of the pigs showed a significant positive autocorrelation when fitting P1, NL, and P3 without IRLS, respectively. Fitting each function with IRLS reduced these percentages to 29.2, 18.2, and 12.5% for P1, NL, and P3, respectively.

For each function without IRLS, average true and estimated DFI were equal, and their mutual correlation equaled unity (Table 2). Looking at parts of the test period, average true and estimated $DFI_{(period)}$ differed somewhat, and correlations ranged from .88 to .98. Correlations were smallest for P1 and highest for P3, which is in line with Table 1.

Table 1. Means (± SD) for residual standard deviation (RSD), coefficient of determination (R^2), and Durban-Watson statistic (DW) per function using SET1[a] (n=192)

	Function[b]					
Trait	P1	NL	P3	$P1_{(IRLS)}$	$NL_{(IRLS)}$	$P3_{(IRLS)}$
RSD	.437 ± .104	.433 ± .102	.419 ± .098	.241 ± .028	.242 ± .028	.234 ± .026
R^2	.472 ± .201	.485 ± .193	.515 ± .181	.816 ± .157	.821 ± .140	.849 ± .094
DW	1.54 ± .43	1.59 ± .43	1.69 ± .42	1.77 ± .28	1.80 ± .31	1.90 ± .29

[a] SET1 was the data set containing only observed feed intake per day records..

[b] P1 was a first degree polynomial, P3 a third degree polynomial, and NL a nonlinear function (see text). Addition of the subscript (IRLS) means that the function was fitted using iteratively reweighted least squares regression.

Fitting functions with IRLS resulted in a similar estimated DFI for the three functions (Table 2). However, for total as well as for parts of the test period, fitting with IRLS always resulted in a larger mean for estimated DFI in comparison with true DFI or estimated DFI without IRLS. A larger mean indicates that more large residuals were caused by a drop in feed intake than by a rise. Correlations between true and estimated DFI with IRLS were for each situation smaller than unity and ranged from 0.78 to 0.97. The effect of IRLS was largest for period 4, as correlations between true and estimated $DFI_{(4)}$ were smallest and most reduced compared to fitting without IRLS. Again, correlations were smallest for the P1 and highest for the P3 function.

Effect of missing FID records on the estimate of DFI per pig (SET2)

Figure 2 shows the results of randomly deleting FID records (alternative one) without IRLS. Deleting up to 70% of the records reduced the correlation between true and estimated DFI only from 1.00 to .96 for each function. Deleting randomly 90% of the records caused a further reduction of the correlation to .84 for P1, .83 for NL, and .60 for P3.

Results of period wise deletions (alternative 2) without IRLS are presented in Figure 3. For P1, deletion of a single or a combination of two periods of records reduced the correlation to values ranging from .62 to .97. Compared to P1, the NL function was particularly susceptible to missing records during period 1. Deleting other periods gave similar results for NL as for P1. For P3, correlations were always lower than for both other functions indicating that P3 is not robust enough to overcome deletions of periods.

Table 2. Means (± SD) for and correlations (r) between true and estimated average daily feed intake (DFI) per pig per function for the total test period and per period, separately, using SET1[a] (n=192)

			Estimated DFI[c]					
Period[b]	Item	True DFI	P1	NL	P3	$P1_{(IRLS)}$	$NL_{(IRLS)}$	$P3_{(IRLS)}$
Total	Mean	2.06 ± .23	2.06 ± .23	2.06 ± .23	2.06 ± .23	2.13 ± .24	2.11 ± .25	2.12 ± .24
	r		1.00	1.00	1.00	.95	.96	.97
1	Mean	1.51 ± .26	1.53 ± .27	1.49 ± .26	1.50 ± .26	1.59 ± .29	1.56 ± .31	1.56 ± .29
	r		.94	.96	.98	.91	.93	.94
2	Mean	1.94 ± .29	1.92 ± .25	1.97 ± .25	1.96 ± .28	1.98 ± .26	2.03 ± .27	2.02 ± .29
	r		.88	.91	.96	.86	.88	.89
3	Mean	2.36 ± .35	2.32 ± .30	2.34 ± .29	2.35 ± .32	2.38 ± .30	2.37 ± .29	2.39 ± .32
	r		.88	.94	.96	.89	.90	.93
4	Mean	2.58 ± .39	2.64 ± .35	2.60 ± .34	2.59 ± .37	2.72 ± .36	2.63 ± .34	2.62 ± .39
	r		.89	.90	.97	.78	.79	.88

[a] SET1 was the data set containing only observed feed intake per day records.

[b] Total was total test period, 1 is d 1 to 25, 2 is d 26 to 50, 3 is d 51 to 75, and 4 was remaining days of test period.

[c] P1 was a first degree polynomial, P3 a third degree polynomial, and NL a nonlinear function (see text). Addition of the subscript (IRLS) means that the function was fitted using iteratively reweighted least squares regression.

With IRLS, the correlation between true and estimated DFI was for each function smaller than unity (Table 2). To separate the effects of missing FID records and IRLS on

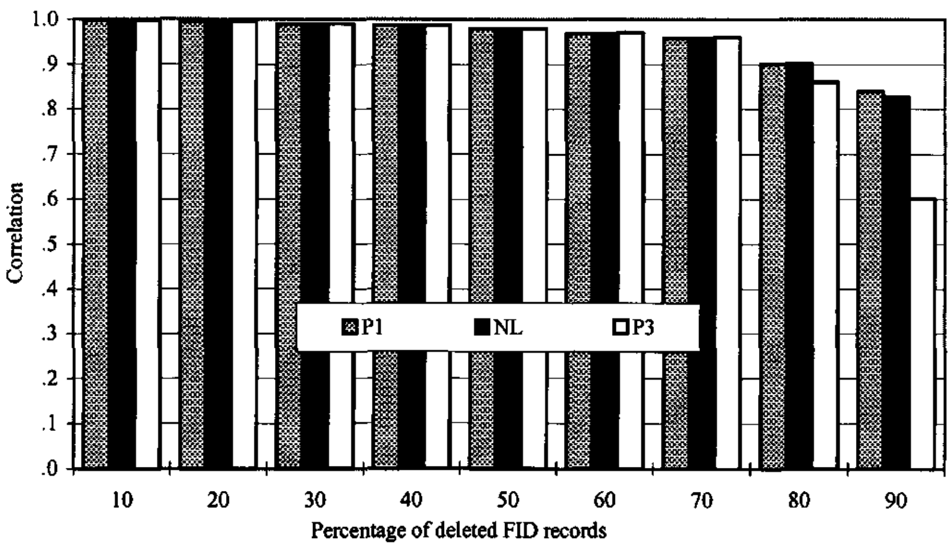

Figure 2. Correlation between true and estimated average daily feed intake per pig, with an increasing percentage of deleted feed intake per day (FID) records and fitting a first (P1) or third (P3) degree polynomial, or a nonlinear (NL) function in SET2 (n=192). SET2 was the data set containing a feed intake per day record for each test day

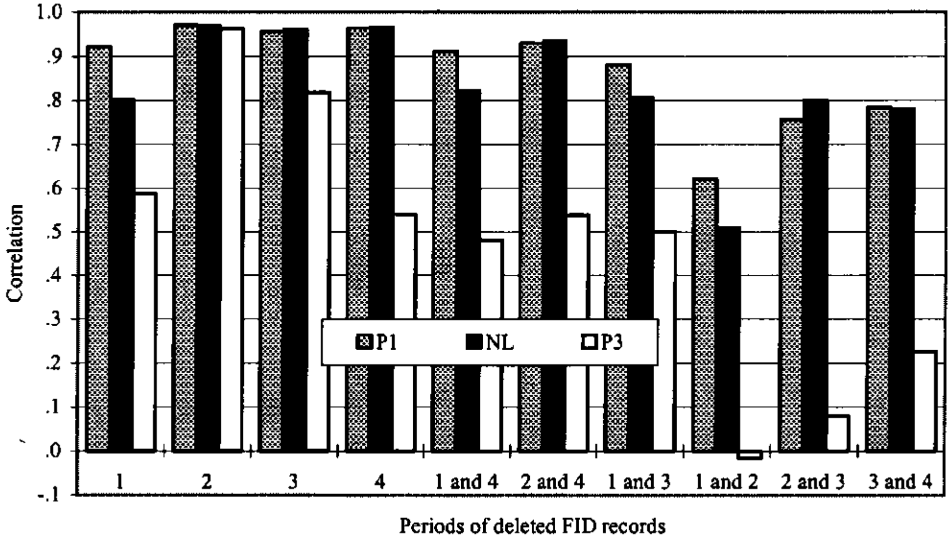

Figure 3. Correlation between true and estimated average daily feed intake per pig, with different periods of deleted feed intake per day (FID) records and fitting a first (P1) or third (P3) degree polynomial, or a nonlinear (NL) function using SET2 (n=192). The test period was divided into three 25-d periods (period 1 to 3; d 1 to 75) and the remaining period (period 4). SET2 was the data set containing a feed intake per day record for each test day.

the correlation between true and estimated DFI, the estimated DFI based on the fit without any deletions of FID records was defined as the true DFI per function. This realized that the correlation between true and estimated DFI equaled unity for each situation without deletions of FID records. Deleting randomly up to 70% of FID records per pig before fitting functions reduced the correlation between true and estimated DFI somewhat more than fitting without IRLS as correlations dropped from 1.00 to .90 for P1, to .85 for NL and to .91 for P3. Period wise deletions of FID records before fitting gave results comparable to fitting without IRLS for P1 and P3. The NL function was susceptible to missing records at the beginning of the test period, leading to lower correlations when period 1 was deleted in comparison to fitting without IRLS.

Without IRLS, mean values of estimated DFI after deleting randomly up to 70% of FID records were for each function similar to true means of DFI. Standard deviations of means increased from .23 to .24 for P1, and .25 for NL and P3 when deleting up to 70% of the records. With IRLS, up to 60% of FID records could randomly be deleted without serious consequences for mean values of estimated DFI and standard deviations. Deleting periods of records caused larger differences between means for true and estimated DFI than random deletions, both for fitting with and without IRLS. Deleting records of period 1 in combination with fitting the NL function caused moderate to severe underestimations of DFI, especially with using IRLS. Deleting periods also caused a more serious increase in estimated standard deviations, especially for P3.

Discussion

Goodness of fit

Fitting the P1 function without IRLS resulted in a larger estimated $DFI_{(period)}$ in period 1 and 4 and in a smaller estimated $DFI_{(period)}$ in period 2 and 3 compared to true $DFI_{(period)}$. This was probably caused by a somewhat reduced feed intake at the start of test period because of adaptation of the animal to its new environment, and a declining increase in feed intake at higher numbers of test days. There was little evidence that the pigs had reached an intake plateau in the present study as the difference between true and estimated $DFI_{(4)}$ was small, although animals were tested up an average body weight of 108 kg. The relatively large number of boars and the absence of castrates in the data set may have contributed to this result.

In literature, only results were found for fitting functions to feed intake data without IRLS. In some literature sources, functions were fitted to total feed intake per week or cumulative feed intake during the test period (e.g., Krieter and Kalm, 1989; Andersen and Pedersen, 1996), which could, consequently, not be compared with present results. Kanis and Koops (1990) and De Boer and Kanis (1991) fitted a second degree polynomial and/or a nonlinear function to weekly averages of daily feed intake of barrows and gilts. Their results ranged from .22 to .33 kg/d for RSD, from .76 to .86 for R^2, and from 1.70 to 2.06 for DW, indicating a better fit than in the present study. The first reason for differences may be that both studies fitted functions to FID records that were averaged per week. This probably eliminated a considerable part of fluctuations among subsequent FID records. Another reason may be that in both papers feed intake was fitted as a function of body weight, as feed intake is more functionally associated with body weight than with age (e.g., Timon and Eisen, 1970; Kanis and Koops, 1990). As there were no regular recordings of body weight throughout the test period, results in this study could not be related to body weight.

Feed intake is a trait that intensely reflects the day-to-day dynamics of an animal's metabolism. Knap (1995) suggested that differences in variation of feed intake over time (RSD) between pigs may be interpreted as differences of the pig's sensitivity to environmental changes. Animals with a high environmental sensitivity react strongly to changes in the environment they must live in. Environmental sensitivity is, therefore, closely connected to the animals' ability to maintain homeostasis (Knap, 1995). Results for RSD might, therefore, be interesting for breeding purposes as well.

Effect of missing FID records on the estimate of DFI per pig

Because pigs differed in length of test period, the percentage of missing FID records per pig ranged from 23 to 33% when deleting 25 FID records, as happened for periods 1 to 3. Results of period 4 should be interpreted with caution: Some pigs were not affected at all (no FID records deleted), whereas on the other hand, some pigs were heavily affected as up to 35 records were deleted. Records in the first part of the test period appeared to be crucial for a good fit of the NL function, especially when fitting was with IRLS. Generally, it was clear that deleting records in periods had a larger impact on estimated DFI than randomly deleting a similar amount of FID records. If the level of estimated DFI is important, for example for computing feed:gain ratio, then IRLS should not be used.

The P1 function estimated DFI better than both others as this function could handle incidental as well as all kinds of periods of missing FID records very well and is recommended. The high correlation between true and estimated DFI of growing pigs shows that a considerable number of FID records may be missing without serious consequences for the estimate of DFI. Consequently, few errors in selecting boars or gilts will be induced by using the presented procedure for estimating DFI. Considering incorrect FID records as missing is, therefore, a good alternative for adjusting data. In practice, restrictions for maximum number and positions of missing FID records are necessary for an accurate estimate of DFI. Results also imply that it is sufficient to record feed intake during parts of the test period, for example every second week (Von Felde et al., 1996), and end up with an accurate estimate for DFI. This would lead to a more efficient use of computerised feeding stations. However, a good system for monitoring a feeding station's functioning is necessary to guarantee good quality feed intake data. Feed intake recording during periods only, e.g., the first or second half of the test period, is not recommended.

Implications

Use of functions to estimate average daily feed intake during the test period is a good strategy to deal with errors and missing values in recorded daily feed intake data. Application of a first degree polynomial function (straight line) is recommended. Furthermore, functions enable a more efficient use of feeding stations by recording feed intake data during e.g., every second week of the test period. A good monitoring system of the functioning of a feeding station is, however, a necessity.

Acknowledgments

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4 Genetic Aspects of the Course of Feed Intake in Relation to Performance of Growing Duroc Pigs

Data from 2,916 growing Duroc pigs were used to study the relationship between feed intake characteristics and performance and carcass traits. Using computerized feeding stations, feed intake data of 494 boars were recorded from 28 to 110 kg of body weight. Per pig, a linear regression was fitted to feed intake per day totals, resulting in a record for the feed intake characteristics intercept, slope, and residual standard deviation of the fit for each pig. These traits represent information that is obtained in addition to average daily feed intake for which feeding stations have primarily been implemented. Heritabilities estimated for daily feed intake, intercept, slope, and residual standard deviation were .48, .32, .32, and .46, respectively. Intercept, slope, and residual standard deviation were positively correlated with average daily feed intake (r_g .41 to .70). Genetic correlations of the three feed intake characteristics with performance and carcass traits ranged from .12 to .17 for feed conversion ratio, .36 to .75 for daily gain, and -.61 to .25 for lean content. The intercept seems the most promising candidate for improving the accuracy of selection for efficient lean growth as it was positively correlated with both average daily gain and lean content.
Keywords: Feed intake curves, Genetic correlations, Heritabilities, Pigs

Introduction

In pig breeding, computerized feeding stations produce information on average daily feed intake of group-housed young pigs. Feeding stations also record information on feeding frequencies and patterns. In general, feed intake behavior traits can be changed substantially by selection, but show low to moderate genetic correlations with performance and carcass traits (e.g., De Haer and De Vries, 1993; Von Felde et al., 1996; Labroue et al., 1997). Therefore, the potential of behavior traits for improving the accuracy of selection for efficient lean growth seems to be limited. However, Hall et al. (1998, 1999) estimated higher genetic correlations between feed intake behavior traits and

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performance traits than the other authors and found a substantial increase in accuracy when feed intake behavior traits were included in the selection index.

Feed intake information across test days may be exploited by fitting feed intake curves to feed intake per test day data. Feed intake per test day is expected to increase after start of the growing period, following a diminishing returns pattern (Krieter, 1986; Kanis and Koops, 1990) and reach a plateau at or before mature weight (Parks, 1982). Eissen et al. (1999) illustrated that a linear function satisfactorily models feed intake for growing pigs that were tested from an average body weight of 28 to 108 kg. Parameter estimates are obtained for feed intake at the beginning of the test period (intercept; feed intake at test day 0), for the linear increase in feed intake during the test period (slope), and for the residual standard deviation of the fit of each animal. Intercept and slope may correlate with performance. Krieter (1986) and Von Felde et al. (1996) found the level of feed intake during early stages of the test period to be more favorably correlated with performance than feed intake during later stages or than average daily feed intake over the entire test period. Residual standard deviation may be interpreted as a measure of within animal variation of feed intake over time (Knap, 1995) and may also correlate with performance.

Temporal drops or rises in feed intake per day cause large residuals when modeling feed intake per day. Large fluctuations have a relatively large impact on a least squares fit of a function (Birch and Fleischer, 1984). Depressions in feed intake per day may be caused by environmental factors (e.g., diseases or vaccination). Iteratively Reweighted Least Squares regression methods (IRLS) protect against undesirable effects of large fluctuations on the fit of functions as large residuals are weighted lower (Birch and Fleischer, 1984; Grossman and Koops, 1988). IRLS may be an appropriate method to correct for disturbing variation in feed intake data.

Objectives of the present study are 1) to estimate genetic parameters of feed intake characteristics (intercept, slope, and residual standard deviation of a linear fit) and their relationships with performance, 2) to quantify the usefulness of IRLS on genetic parameter estimates, and 3) to discuss possible benefits of feed intake characteristics for pig breeding.

Materials and methods

Animals

Data of growing Stamboek Duroc pigs recorded at one nucleus breeding herd between April 1995 and April 1997 were obtained. In total, the data set contained information on

Table 1. Number of pigs with a record by trait (diagonal) and by combination of two traits (off diagonal)

Traits	Traits			
	Feed intake traits, FCR[a]	Daily gain, backfat thickness	Lean content	Intramuscular fat content
Feed intake traits, FCR[a]	494	494	103	100
Daily gain, backfat thickness		2912	370	368
Lean content			374	363
Intramuscular fat content				372

[a] FCR = feed conversion ratio

1,524 boars and 1,392 gilts, being progeny of 45 sires and 268 dams in 477 litters. For each animal the complete pedigree up to fourth ancestor generation was available. A total of 3,524 pedigree animals was considered in the analysis. Tables 1 and 2 summarize the structure of the data set as used in the final analyses

Table 2. Distribution of records over sexes, litters, sires, and dams per trait

Item	Traits			
	Feed intake traits, FCR[a]	Daily gain, backfat thickness	Lean content	Intramuscular fat content
No of gilts tested	-	1,389	101	100
No of boars tested	494	1,523	273	272
No of litters tested	230	477	256	253
No pigs tested per litter	2.15 ± 1.23	6.10 ± 2.31	1.46 ± 1.31	1.47 ± 1.27
No of sires	40	45	41	41
No pigs tested per sire	12.35 ± 7.89	64.71 ± 31.78	9.12 ± 8.04	9.07 ± 7.78
No of dams	165	268	177	173
No pigs tested per dam	2.99 ± 2.03	10.86 ± 7.22	2.11 ± 1.89	2.15 ± 1.77

[a] FCR = feed conversion ratio

Feed intake traits

Preferentially two male pigs per litter were selected for individual feed intake recording. Selection within litter was on exterior (visual appraisal); in fact these young boars were potential breeding boars. Incidentally, more pigs per litter were selected in order to fill up pens, particularly when there were no pigs available from other litters. Pigs were tested in groups of 10 to 12 per pen. Ad libitum feed intake of 592 pigs was recorded using 12 IVOG®-feeding stations (Insentec, Marknesse, The Netherlands). Records on feed intake per visit were checked for errors by incorrect feeder weights, using algorithms described by Eissen et al. (1998). Subsequently, records on feed intake per visit were summarized to feed intake per pig per day records. Feed intake per day records that contained error-visits were eliminated.

In total, data of 494 out of the 592 pigs were used for the analysis. Feed intake data of 82 animals were removed because they had no record for body weight at the end of test due to death or illness (29 animals) or they had no feed intake data recorded during the first 35-70 days of their test due to malfunctioning of the recording system (53 animals). Eleven pigs were removed from the analysis due to incomplete data based on criteria derived from Eissen et al. (1999). Five of the remaining 499 pigs were gilts, which were, therefore, removed from the data as well. For the 494 pigs, test started and ended at an average body weight of 28 (SD = 4.2) and 110 kg (SD = 9.1), respectively. Feed intake testing was based on body weight and ended simultaneously with performance testing.

A linear regression was fitted to feed intake per test day records per individual pig (Eissen et al., 1999):

$$FID(t) = intercept + slope \times t$$

where FID(t) is the estimated feed intake at test day t. Intercept and slope are function parameters. The fit of a linear regression resulted in a record for intercept, slope, and residual standard deviation for each pig. For each pig, average daily feed intake was computed by averaging all FID records (Eissen et al., 1999).

Iteratively reweighted least squares regression (IRLS)

Linear regression was also performed using IRLS (Proc NLIN, using Gauss-Newton; SAS, 1990). Details about linear regression with IRLS to exclude undesirable effects of large residuals have been described previously (Eissen et al., 1999). Applying IRLS gave a second set of records for average daily feed intake and intercept and slope of the fit for each of the 494 pigs.

Performance and carcass traits

Average daily gain and backfat thickness was obtained from all 2,916 pigs, except four. Pigs were group in pens during performance test. The end of the performance test was based on weight. Pigs with recorded feed intake data were tested to an average body weight of 110 kg, which is referred to as weight test class 1. Pigs without feed intake data were tested to an average body weight of 103 kg (SD = 9.5), which is referred to as weight test class 2. Daily gain was computed based on body weight and age at end of test. Backfat thickness was the mean of three ultrasonic measurements along the back. Individual feed conversion ratio was computed for the 494 pigs with feed intake data as average daily feed intake divided by daily gain during the test period.

Animals were slaughtered one week after performance testing. Carcasses were dissected one day after slaughter. From April 1995 to September 1996, the right carcass halves were dissected into trimmed major joints according to the Dutch standard dissection method (Bergström and Kroeske, 1968; Walstra, 1980), referred to as method of dissection 1. Lean content was the sum of weights of trimmed major joints plus meat scraps, divided by cold weight of that carcass half. From September 1996 to April 1997, both carcass halves were dissected according to the new EU reference dissection method (Walstra and Merkus, 1995), except that the hind shank stayed with the ham and the front shank stayed with the shoulder (method of dissection 2). For method 2, lean content was defined as the sum of weights of hams, loins and shoulders, all without subcutaneous fat but not deboned, divided by the cold carcass weight. In total, 167 pigs were dissected according to method 1 and 207 according to method 2.

Intramuscular fat content was measured on 372 animals by petroleum-ether extraction, in a 2 cm-thick meat slice taken from the *M. Longissimus* at the last rib of the loin. Samples of constant size (diameter of samples = 4 cm) were used. For lean and intramuscular fat content, one pig per litter was selected. In general, the first pig of a litter not meeting the selection criteria for performance and exterior was dissected to determine lean and intramuscular at content. Males were more often dissected than gilts as most males finished their performance test earlier because of faster growth. Occasionally, two or more pigs per litter were dissected.

Statistical analysis

The statistical model for each trait is shown in Table 3. All models have the following basic form:

$$y = Xb + Wp + Za + e$$

where y is the vector of observations, b is the vector of fixed effects, p is the vector of random litter effects, a is the vector of random additive genetic values of animals, e is the vector of random residuals, and X, W, Z are incidence matrices relating observations to the effects included in the model.

Variance components were estimated using the VCE program of Groeneveld (1994; version 4.2). Heritability and common environment estimates (± SE) for average daily gain and backfat thickness and the mutual genetic and error correlations were estimated in a bivariate run. For the other traits, heritability and common environment estimates were obtained from the results of multi (three) trait analyses with average daily gain and backfat thickness included in each analysis to account for selection. Genetic and error

Table 3. Models of analysis used for different traits [a]

Trait	Fixed effects or covariates[a]						Random effects	
	Year-month[b]	Sex[c]	Method of dissection[d]	Weight test class[e]	Start test weight (covariate)[f]	% of test days (covariate)[g]	Litter[h]	Individual additive genetic value
Feed intake traits[i]								
- Daily feed intake, intercept of fit	x				x		x	x
- Slope of fit	x						x	x
- Residual standard deviation	x				x	x	x	x
Performance traits								
- Feed conversion ratio	x				x		x	x
- Daily gain	x	x		x			x	x
- Back fat thickness	x	x					x	x
Carcass traits								
- Proportion of lean	x	x	x					x
- Intramuscular fat content	x	x						x

[a] The fixed effect year-month was always included in the model, independent of level of statistic significance. The other fixed effects and covariates were only included in the model when relevant and when the effect was statistically significant ($p < .05$). Significance of effects was tested using SAS Procedure GLM (SAS, 1990).

[b] Year-month (25 levels: 9504, 9505,...9703, 9704) of finishing test for feed intake and performance traits and year-month of slaughter for carcass traits.

[c] Feed intake only available from boars.

[d] Method of dissection (two levels: 1 and 2; see text).

[e] Weight test class (two levels: 1 and 2, see text).

[f] There was variation in body weight at the start of feed intake recording due to the limited number of pens with a feeding station.

[g] Percentage of total number of test days with a record for feed intake. A lower percentage reduced the residual standard deviation estimate.

[h] The litter effect was not taken into account in the model applied to the carcass traits because only a few pigs originated from the same litter.

[i] The same models were used for feed intake traits estimated with or without using IRLS.

correlations between average daily gain / backfat thickness on the one hand and all other traits on the other were obtained from the same results. Genetic and error correlations among the remaining traits were estimated in runs of four traits, with average daily gain and backfat thickness again included in each analysis. Standard errors of genetic correlations were approximated by the method of Robertson (1959).

The genetic and error correlation matrices for some combinations of traits had negative eigenvalues. Positive definite matrices were obtained by setting negative eigenvalues to 0 (Hayes and Hill, 1981). Phenotypic correlations were computed from estimated heritabilities and genetic and error correlations per combination of two traits.

Results

Figure 1 shows that animals with a large estimate for intercept and therefore a relatively high daily feed intake during the first part of the test period had a similar daily feed intake as the average animal towards the end of the test period. In contrast, animals with a large slope estimate had a relatively high daily feed intake during the second half of the test period with a similar daily feed intake as the average animal in the beginning. Animals with a large estimate for residual standard deviation had a daily feed intake somewhat higher than average throughout the test period. Statistics for feed intake, performance, and carcass traits are presented in Table 4. The use of IRLS resulted in somewhat larger means for average daily feed intake and slope of the fit.

Heritabilities and genetic correlations

Heritabilities (Table 4) for feed intake traits were moderate to high, with values ranging between .19 and .48. Values for c^2 ranged from .01 to .13. The use of IRLS resulted in a similar / somewhat larger phenotypic variance for average daily feed intake

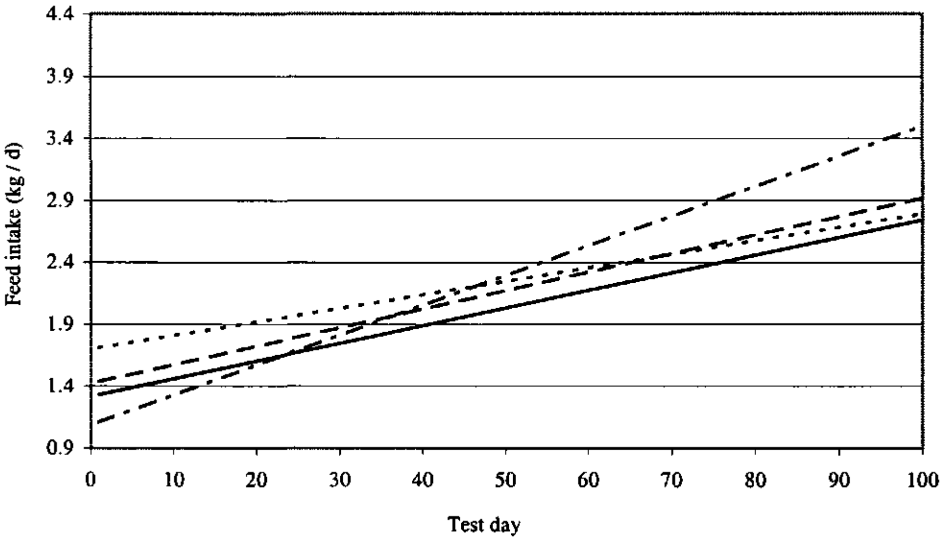

Figure 1. Linear regression fitted to the average feed intake per test day records of all animals (——), and of the 50 animals with the largest estimate for intercept (·······), slope (– · – ·) and residual standard deviation (– – – –).

Table 4. Phenotypic means (± SD) and variances (σ^2_p), heritabilities (h^2 ± SE), and common environment effects (c^2 ± SE) of feed intake, performance, and carcass traits

Trait	Symbol[a]	Unit	Mean ± SD	σ^2_p	h^2 ± SE	c^2 ± SE
Average daily feed intake (28-110 kg)	DFI	kg	2.03 ± .23	.042	.48 ± .00	.11 ± .00
Average daily feed intake with IRLS	DFII	kg	2.08 ± .24	.043	.43 ± .00	.13 ± .00
Intercept of fit	A	kg	1.22 ± .25	.052	.32 ± .01	.07 ± .00
Intercept of fit with IRLS	AI	kg	1.23 ± .24	.045	.19 ± .00	.13 ± .00
Slope of fit	B	kg / d	.0161 ± .0051	.020[b]	.32 ± .05	.07 ± .02
Slope of fit with IRLS	BI	kg / d	.0169 ± .0053	.022[b]	.36 ± .00	.03 ± .00
Residual standard deviation of fit	RSD	kg	.43 ± .11	10.00[b]	.46 ± .00	.01 ± .03
Feed conversion ratio (28-110 kg)	FCR	kg / kg	2.49 ± .18	.024	.25 ± .00	.13 ± .00
Average daily gain (birth-104 kg)	ADG	g / d	590.3 ± 55.8	2490.1	.42 ± .01	.09 ± .00
Backfat thickness	BF	mm	11.99 ± 1.90	3.45	.49 ± .00	.08 ± .05
Carcass lean content	LC	%	54.53 ± 5.10	3.36	.38 ± .00	
Intra muscular fat content	IMF	%	2.72 ± .99	.68	.50 ± .10	

[a] Symbols used in following tables

[b] Variance estimates (x 1000)

and slope of the fit, and in a smaller phenotypic variance for intercept. Both, h^2 and c^2 estimates were affected by IRLS, however in opposite direction: an increase in h^2 was combined with a decrease in c^2 and vice versa.

Genetic correlations between feed intake traits estimated with and without IRLS were ≥ .99 (Table 5). The genetic correlation between intercept and slope estimates ranged from -.36 to -.48, indicating that a high initial feed intake is associated with a lower increase during the test period. Intercept and slope estimates showed a moderate to high positive genetic correlation with estimates of average daily feed intake.

Genetic correlations of feed intake traits with performance and carcass traits were very similar for fitting the linear regression with and without IRLS. Correlations are, therefore, only presented for fitting a linear regression without IRLS (Table 6). Residual standard deviation showed a positive correlation with each of the other feed intake traits. Average daily feed intake, intercept, slope, and residual standard deviation were positively correlated with feed conversion ratio, average daily gain, and backfat thickness. Correlations varied from low (.05) to high (.88). Average daily feed intake, slope, and residual standard deviation showed a negative genetic relationship with lean content and a

Table 5. Genetic (± SE; above diagonal) and phenotypic correlations (below diagonal) among feed intake traits

Trait[a]	DFI	DFII	A	AI	B	BI
DFI		.99 ± .00	.66 ± .01	.62 ± .01	.41 ± .03	.53 ± .00
DFII	.92		.53 ± .01	.50 ± .01	.54 ± .02	.70 ± .00
A	.45	.38		.99 ± .00	-.39 ± .04	-.39 ± .00
AI	.41	.33	.85		-.48 ± .04	-.36 ± .00
B	.40	.40	-.63	-.53		.99 ± .00
BI	.39	.56	-.47	-.61	.82	

[a] For abbreviations see Table 4.

positive relationship with intramuscular fat content, whereas intercept showed relationships of opposite sign. Correlation among feed intake traits in Tables 5 and 6 could differ somewhat as genetic and error correlation matrices were made positive definite for both combinations of traits, separately.

Table 6. Genetic (± SE; above diagonal) and phenotypic correlations (below diagonal) among feed intake, performance and carcass traits

Trait[a]	DFI	A	B	RSD	FCR	ADG	BF	LC	IMF
DFI		.65 ± .01	.41 ± .03	.70 ± .00	.43 ± .01	.88 ± .00	.52 ± .00	-.34 ± .01	.15 ± .03
A	.44		-.38 ± .04	.39 ± .01	.16 ± .01	.61 ± .01	.05 ± .01	.25 ± .01	-.30 ± .05
B	.40	-.62		.26 ± .02	.17 ± .04	.36 ± .06	.50 ± .02	-.61 ± .02	.71 ± .09
RSD	.24	.28	-.08		.12 ± .00	.75 ± .00	.58 ± .00	-.54 ± .00	.02 ± .02
FCR	.26	.21	.04	.22		.13 ± .02	.36 ± .01	-.34 ± .01	-.16 ± .04
ADG	.80	.32	.35	.13	-.25		.49 ± .01	-.26 ± .01	.21 ± .07
BF	.58	.12	.36	.13	.10	.52		-.81 ± .00	.11 ± .03
LC	-.38	-.01	-.32	-.18	-.10	-.29	-.64		-.47 ± .02
IMF	.32	-.02	.37	.09	.19	.19	.40	-.41	

[a] For abbreviations see Table 4.

Discussion

Aim of this study was to estimate and discuss relationships of feed intake characteristics with performance and carcass traits. Estimates for genetic parameters were generally similar in sign and magnitude to values in literature for average daily feed intake and performance and carcass traits (Van Steenbergen et al., 1990; Ducos et al., 1993; Cameron and Curran, 1994; De Vries et al., 1994; Hermesch, 1996; Von Felde et al., 1996; Labroue et al., 1997). This suggests that bias in genetic parameters due to non-random selection procedures of animals for the recording of feed intake and carcass traits was limited. Although the size of the data set was limited, standard errors estimated for h^2 and c^2 by VCE were extremely small. Heritability and c^2 estimates were also obtained after bivariate and univariate analysis, and also after scaling of traits. This resulted in similar h^2 and c^2 estimates, however in different standard errors. Results for standard errors should therefore be interpreted with care.

Iteratively reweighted least squares regression (IRLS)

IRLS was studied as a possible method to correct for disturbing variation in feed intake data (for example a drop in feed intake due to an infection). In literature, no references were found that used IRLS in a genetic analysis. Grossman and Koops (1988) showed positive effects of weighing individual data records on the fit of growth curves in chickens. The effect of IRLS on heritabilities of feed intake traits and on genetic correlations of these traits with production traits was limited. Main reason for absence of positive effects of IRLS (e.g., higher h^2 estimates for feed intake traits) in the present study may be the large number of feed intake per day records per pig. One or a few outlier values per pig may only have a limited effect on the fit of a linear regression, as pigs were tested for an average of 100 days. The use of IRLS will not be discussed further here.

Feed Intake Characteristics

To our knowledge, genetic parameters for intercept, slope, and residual standard deviation of a linear fit to feed intake data have not been published before. Heritability estimates showed that each of these traits may be changed by selection.

Pigs with a large intercept have a high feed intake particularly during the early stage of the test period (Figure 1). Consequently, these pigs will have a high weight gain during this period. Moreover, intercept has positive genetic correlations with average daily gain and lean content, which means that these pigs grow lean (Table 6). All these aspects will result in relatively high maintenance costs during the test period. In contrast, animals with a large slope show a high feed intake (and consequently weight gain) during the later stage of the test period (Figure 1) and grow relatively fat, as indicated by the genetic correlations of Table 6. Both will result in relatively low maintenance costs during the test period. However, fat deposition requires more feed per weight than lean deposition (Webster, 1977). The overall effect of maintenance costs and composition of growth resulted in a similar positive genetic correlation of intercept and slope with feed conversion ratio (r_g = .16 / .17; Table 6). A large residual standard deviation indicates a relatively large day-to-day variation in feed intake and was genetically correlated with fast, however, relatively fat growing pigs (Table 6).

Krieter (1986), Von Felde et al. (1996), and Hall (1997) studied average daily feed intake during early, middle, and late stages of the test period in relation to average daily feed intake over the entire test period and performance and carcass traits. Krieter (1986) and Von Felde et al. (1996) estimated more favorable genetic correlations for daily feed intake during early stages with feed conversion ratio, backfat thickness, and lean content compared to daily feed intake during later stages or daily feed intake over the entire test period. These results are in agreement with present results for intercept and slope (Table 6). Hall (1997) did not find an effect of stage of feed intake recording on the genetic correlation with total feed conversion ratio and estimated only a small effect of stage on backfat thickness and average daily gain, which was favorably for the early and middle stage of recording, respectively. Differences in performance testing may have contributed to differences between the three studies as Hall (1997) tested pigs during a 50 kg period whereas both others tested pigs during about 70 kg of body weight. Average daily feed intake over the entire test period showed the highest correlation with daily gain in all three studies.

Present results indicate that it seems beneficial to select pigs with a high feed intake (growth rate) during the early stage of the test period for selection of efficient lean pigs. This is confirmed by Hermesch (1996) who found that growth from week 3 to 18 of age was more favorably correlated with leanness at slaughter weight than growth from week 18 to 22. Barbato (1994) found similar results in poultry. Chickens were selected five generations for either average daily gain from day 1 to 14 or from day 1 to 42 of age and were slaughtered at 42 days of age. Both selection lines showed a similar average daily feed intake and gain from day 1 to 42 and ate more and grew faster than a control line. Chickens selected for average daily gain from day 1 to 14 ate more during this stage of the total period than the other selected line and ended up much leaner at 42 days.

Inclusion of feed intake characteristic information in selection indices in order to select for an efficient lean growth might lead to a reduction in intramuscular fat content as intercept was negatively correlated with intramuscular fat content and slope and residual standard deviation showed a positive genetic correlation. In general, intramuscular fat content is considered an optimum trait, as a low value results in a low meat tenderness (De Vol et al., 1988) and a high value results in undesired marbling (Hovenier et al., 1993). Given the present level of 2.72% intramuscular fat, short-term negative effects of a decrease in intramuscular fat content are probably limited in offspring of this Duroc population (De Vol et al., 1988; Hovenier et al., 1993). However, for long term effects and for populations with lower current levels of intramuscular fat, expected changes in intramuscular fat content should be considered in breeding decisions.

Intercept, slope, and residual standard deviation represent information that is obtained in addition to average daily feed intake, which is the information feeding stations have primarily been implemented for. The potential of intercept, slope, and residual standard deviation for improving accuracy of selection was studied by including these traits one by one in an own performance selection index containing the traits daily gain, backfat thickness, and average daily feed intake. The aggregate genotype of these indices consisted of daily gain, lean content, and average daily feed intake with economic weights of .178, 3.0, and –50.0, respectively, based on De Roo (1988). Calculations are based on estimated heritabilities (Table 4) and genetic correlations (Table 6) of the present study. Inclusion of intercept, slope, and residual standard deviation in the selection index raised the accuracy of selection from .58 to .60 (intercept), .59 (slope), and .61 (residual standard deviation). Each selection index resulted in a negative predicted selection response for average daily feed intake, which is undesirable as feed intake could be a limiting factor both for lean growth and for lifetime productivity of lean sows in future (e.g., Webb and Curran, 1986; Kanis, 1990). Halving the economic weight for average daily feed intake to –25.0 resulted in a positive predicted selection response for average daily feed intake of each index. For this situation, inclusion of intercept in the index gave the largest increase in accuracy from .56 to .60.

It may be concluded that intercept, slope, and residual standard deviation are valuable traits to gain more selection response from the use of feeding stations without extra costs. The intercept seems the most promising candidate as it was positively correlated (genetically) with both average daily gain and lean content.

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5 Ad Libitum and Optimum Feed Intake of Different Pig Genotypes

The objective of this study was to elucidate the desirable direction of selection for feed intake capacity of growing pigs. For pig breeding organizations, it is important that end product genotypes have a feed intake capacity that is close to their economic optimum. An experiment was set up in order to study relationships between feed intake and protein (PD) and lipid (LD) deposition. A linear plateau relationship between PD and feed intake was assumed to derive the optimum feed intake for the early (25-65 kg), middle (65-95 kg), and late growth phase (95-125 kg), separately. For each weight range, relationships between feed intake and PD and LD were studied for five genotypes (three dam lines and two end products) and three sexes. In total, 1019 animals had an estimate for PD, LD and daily feed intake. Feed intake capacity was lower than optimum more often for gilts and boars than for castrates within genotype, and more often for end product genotypes than for dam line genotypes. Feed intake capacity of end product gilts was below or close to optimum during the growing period from 25-125 kg. It seems therefore beneficial to select for a higher ad libitum feed intake in combination with selection for other production traits. Moreover, it is recommended to house sexes separately during the growth period.
Keywords: Growing pigs, Feed intake capacity, Protein deposition, Optimum feed intake

Introduction

Ad libitum feed intake capacity of growing pigs is generally considered as a trait with an optimum with respect to feed efficiency. An optimum occurs where savings in total maintenance requirements from faster growth are offset by increased lipid deposition (Vanschoubroek et al., 1967; Webb, 1989). Performance testing and selection programs have improved lean content and feed conversion ratio considerably over the past decades. Some of these programs, giving a high emphasis to efficiency rather than to rate of lean growth on ad libitum feeding, have led to a reduction in daily feed consumption (Webb, 1989; Cameron and Curran, 1994). Furthermore, as lean deposition potential is expected

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to continue to increase through genetic selection or better health management, energy intake is likely to become the limiting factor for more body lean deposition (Schinckel and De Lange, 1996). This means that feed intake capacity may be or may become lower than optimum and become a limiting factor for a further increase in lean growth rate during at least a part of the growing period.

The concept of a linear-plateau response of protein deposition to energy intake, as proposed by Whittemore and Fawcett (1976) is commonly used to describe the relationship between energy intake and protein deposition (PD) and lipid deposition (LD). Over recent decades the concept has been further developed and improved (e.g., De Greef and Verstegen, 1995). It is generally accepted that there is a linear effect of energy intake on PD and LD when energy intake is greater than the amount needed for maintenance and less than the amount required for maximizing PD. The economically optimum energy intake generally equals the minimum level of intake to reach maximum PD (PDmax; Kanis and De Vries, 1992; Kanis, 1995; Schinckel and De Lange, 1996). Kanis (1995) showed in a simulation study that, using Dutch feed costs and carcass prices, the highest financial returns per pig place per year were indeed accomplished when feed intake just reached PDmax during the complete growing period up to 110 kg of body weight. The optimum intake is closely related to the growth potential of pigs, i.e., genotype, sex and metabolic state (Quiniou et al., 1996).

The objective of this study was to determine the desirable direction of selection for feed intake capacity. For pig breeding organizations, it is important that end product animals have a feed intake capacity that is close to optimum. An experiment was set up to characterize commercial lines of pigs for linear-plateau concept parameters and feed intake capacity within the weight range of 25-125 kg. The actual level of ad libitum feed intake of genotypes and sexes was studied in relation with the optimum level.

Material and methods

Experimental design

Data were recorded on 1143 growing pigs at the experimental farm of IPG in Beilen, from February 1996 till February 1999. The experiment was performed with pigs of a commercial purebred Dutch Landrace dam genotype (genotype 1; females, castrates, males), two commercial Landrace / Yorkshire based crossbred dam genotypes (genotypes 2 and 3; females), and two commercial Landrace / Yorkshire / Duroc based end product genotypes (genotypes 4 and 5; females and castrates). Accordingly, there were nine genotype / sex combinations within the experiment. Genotype 2 and 3 animals were progeny of genotype 1 type sows and genotype 4 and 5 animals were progeny of genotype 2 and 3 type sows, respectively. During the experimental period, pigs were either fed ad libitum or about 75 or 60% of expected ad libitum intake at a certain weight (restricted1 and restricted2, respectively). Both restricted feeding levels were equal for each genotype and sex. The growing period 25-125 kg was divided into three body weight ranges: 25-65 kg, 65-95 kg and 95-125 kg (Figure 1). Animals starting the experiment at 65 or 95 kg were fed according to restricted1 during the pre-experimental period from 25 kg of body weight onwards.

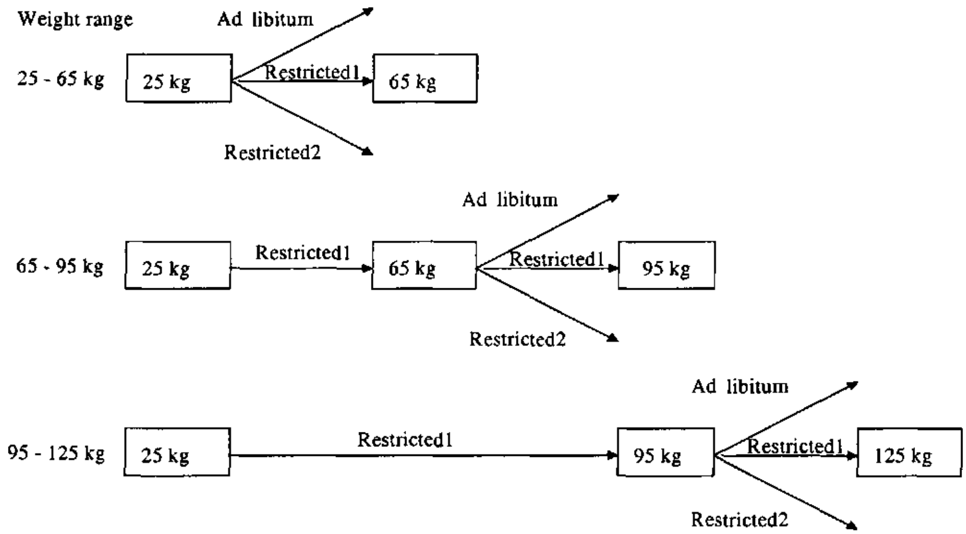

Figure 1. Schematic overview of the experimental set up per combination of genotype and sex for each of the three weight ranges.

At the start of the experiments at 25, 65, or 95 kg, three littermates of the same sex were randomly allocated to the three feeding levels. Five to eight pigs of the same genotype / sex / weight range / feeding level combination were housed in one group to allow social interactions during the experimental period. Ad libitum and restrictedly fed animals were housed in different units of the same barn. Feed intake of ad libitum fed animals was recorded with an IVOG®-feeding station (Insentec, Marknesse, The Netherlands). Feed restricted animals were hand fed twice a day. During eating (two times 30 minutes per day), pigs were fixed in boxes to ensure correct recording of feed intake per animal. Restrictedly fed pigs had access to water only during eating, whereas ad libitum fed animals had free access to water all day. Pigs were weighed once a week during the experiment. Feed allowances for feed restricted animals were adjusted after each weighing to the expected gain for the next week. All pigs within a pen received the same amount of feed, which was based on the average pen body weight. Feed refusals were collected and weighed once a week. Feed allowance corrected for refusals was used in the analysis. During the pre-experimental periods from 25 up to 65 or 95 kg, animals were weighed at approximately three-week intervals and feed allowances were adjusted to the expected gain for the following three weeks. Feed was supplied twice a day in a trough during the pre-experimental period without fixing the animals. The level of restriction may therefore differ between animals during the pre-experimental period.

High quality commercial diets that were used during the course of the experiment were iso-energetic and had a similar composition. The diets used from 25 to 65 kg of body weight contained 15.1 MJ DE / kg, 189 - 191 g crude protein / kg, and 10.5 - 10.6 g lysine / kg. The diets used from 65 to 125 kg of body weight contained 15.1 MJ DE / kg, 170 to 187 g crude protein / kg, and 9.0 g lysine / kg. The supply of amino acids, minerals, vitamins etc. was assumed always to be sufficient (ARC, 1981). Minimum room temperature was maintained between 17 and 18 °C during the experiment. Maximum room temperature depended on the outside temperature. Routine management procedures were followed in taking care for the animals.

All animals in a pen were slaughtered at the same day. According to the set up of the experiment, pigs were slaughtered in the week the average body weight of a pen of pigs reached the target weight. All carcasses were dissected into major joints the day after slaughter. Two of the 5-8 litters per genotype / sex / weight range combination were randomly selected for whole body chemical analysis of protein and lipid content; two pigs per pen, therefore, were analyzed chemically. For most combinations of genotype / sex / weight range, measurements were repeated at least once within the experiment. This resulted in a minimum of about ten animals per combination of genotype / sex / weight range and feeding level with known results of dissection, of which about four animals had a known chemical composition (Table 1). Animals with a record for chemical composition were used to predict chemical composition of animals at the start and end of the experiment (see under 'calculations and statistical analyses'). At 25 kg of body weight, 22 pigs were slaughtered and analyzed chemically to obtain data for the composition of animals starting at 25 kg.

Measurements

At the beginning of each experimental period, animals were given a 3-4 day adaptation period to get used to the new pen mates and feeding system. After the adaptation period, each animal was weighed (start body weight) and backfat thickness was measured ultrasonically on six points (three on each side; start backfat thickness) for animals of 65 and 95 kg. The day before slaughter, final body weight and backfat thickness were measured. Average start and final backfat thickness were used in the analysis. At slaughter, animals were killed by electrical stunning. During slaughter the scalded, scraped and eviscerated carcass, including head and feet, was split longitudinally. From animals selected for chemical analysis, organs and blood were collected during slaughter. The contents of the gastro-intestinal tract were removed. Blood and organs (together referred to as organs fraction) were weighed together for each pig, and stored at -20° C.

Table 1. Number of pigs with data for average daily feed intake, protein deposition and lipid deposition per combination of genotype, sex, feeding level, and weight range

Genotype	Sex	Feeding	25 kg	25-65 kg		65-95 kg		95-125 kg	
		Level[a]	C[b,c]	T[b]	C[b]	T[b]	C[b]	T[b]	C[b]
Genotype 1	Females	AL		29	8	14	4	7	2
		R1		28	8	14	4	15	4
		R2		26	7	16	4	15	4
	Castrates	AL	5	9	4	8	2	7	2
		R1		10	4	14	4	2	2
		R2		8	3	14	4	8	2
	Males	AL		13	4	7	3	12	3
		R1		14	5	18	6	16	5
		R2		18	5	15	5	13	5
Genotype 2	Females	AL		7	4	12	4	14	4
		R1		4	4	11	4	16	2
		R2		8	4	12	3	16	4
Genotype 3	Females	AL	6	14	4	8	2	8	2
		R1		15	4	6	2	8	2
		R2		14	3	6	2	7	1
Genotype 4	Females	AL		11	3	16	6	12	3
		R1		8	4	18	6	15	4
		R2		9	3	18	5	15	4
	Castrates	AL	6	9	4	12	3	9	3
		R1		9	4	14	4	10	4
		R2		11	4	16	4	11	4
Genotype 5	Females	AL	2	14	4	10	4	15	4
		R1		16	3	12	4	16	4
		R2		15	4	12	4	14	4
	Castrates	AL	3	14	4	10	3	8	3
		R1		16	4	12	4	12	4
		R2		16	4	12	4	16	4
Total			22	365	116	337	104	317	89

[a] AL = ad libitum; R1 = restricted1 (75% of ad libitum); R2 = restricted2 (60% of ad libitum)

[b] T = total number of animals with data; C = number of animals with data from chemical analysis after slaughter.

[c] All animals were fed ad libitum till 25 kg of body weight.

The day after slaughter both carcass halves were weighed. Further, hams, loins and shoulders were separated from the carcass according to the new EU reference dissection method (Walstra and Merkus, 1995), with the difference that the hind shank stayed with the ham and the front shank stayed with the shoulder. Subcutaneous fat was trimmed off from each joint. For pigs selected for chemical analysis, all dissected parts of the left carcass half were collected and stored at -20° C. Only for pigs slaughtered at 25 kg of body weight, the whole carcass was used for chemical analysis. The frozen carcass and organs fractions were cut into pieces and homogenized separately in a commercial butcher's mincer. Each fraction was sampled for chemical analysis (nitrogen and lipid). Nitrogen content was measured using the Kjeldahl technique, lipid content was determined by petroleum-ether extraction. Total chemical body composition (percentages of protein and lipid) was computed from the chemical composition and weights of carcass and organs fractions.

Calculations and statistical analyses

Ad libitum feed intake data recorded with IVOG®-feeding stations were checked per visit for incorrect recording of feeder weight or time, using algorithms described by Eissen et al. (1998). Subsequently, records on feed intake per visit were summarized to feed intake per pig per day records. Feed intake per day records that contained error-visits were eliminated. A linear regression was fitted to feed intake per day records per individual pig to compute average daily feed intake during the experimental period (Eissen et al., 1999).

Obvious outliers for various traits (ratios smaller or larger than group mean ± 3 x standard deviation) were excluded from the data (14 animals). Incidentally, pigs had missing values for some traits. Missing values were replaced by estimates for three clusters. Firstly, because backfat thickness was an important predictor of the start body composition at 95 kg, start backfat thickness at 95 kg was estimated for 23 (out of 363) animals using body weight and age information of animals. The second and third cluster of missing values concerned animals that were analyzed chemically. Body weight of eight out of 22 animals slaughtered at 25 kg was estimated using age and carcass weight information. Besides, total weight of the organs fraction was estimated for 17 out of 325 animals selected for chemical analyses using in vivo and post mortem information.

Below, it is described how chemical body composition of animals at the start and end of the experiment was predicted, how PD and LD records were calculated subsequently, and finally, how parameters of the linear plateau relationship were estimated. Chemical body composition of pigs slaughtered at 25 kg of body weight was used to predict the chemical body composition of animals starting the experiment at 25 kg. Similarly, data on chemical body composition of pigs which were fed according to restricted1, slaughtered at 65 or 95 kg, and analyzed chemically were used to predict chemical body composition of pigs starting at 65 or 95 kg, respectively. For prediction of chemical body composition of animals at the start, linear regression relationships of chemical body composition on age, body weight, and backfat thickness were established per level of body weight:

$$Y = \beta_0 + G \times S + \beta_1 \text{ age} + \beta_2 \text{ body weight} + \beta_3 \text{ backfat thickness} + \text{Error} \qquad [1]$$

Where Y = percentage of protein or lipid of an individual pig; G = genotype; S = sex. Backfat thickness could only be used at 95 kg because 74 animals starting at 65 kg were not measured for backfat at 65 kg and all 25-kg pigs did not have backfat thickness recordings. The interaction between genotype and sex was not included in the model used to predict the body composition at 25 kg because chemical body composition was only known for animals of four of the nine genotype / sex combinations (Table 1).

Linear regression relationships of final chemical body composition on in vivo and post mortem measurements were established within animals analyzed chemically to predict final chemical body composition of all pigs slaughtered. Animals that were analyzed chemically were representative for other animals of the same weight range and feeding level combination concerning body weight and backfat thickness (Table 2). The regression relationships were established per combination of weight range and feeding level, in order to keep data of the several weight ranges and feeding levels independent. The initial model included the following traits:

$$Y = \text{model [1]} + \beta_4 \text{ carcass weight} + \beta_5 \text{ lean mass} + \beta_6 \text{ fat mass} \qquad [2]$$

Where Y = percentage of protein or lipid; lean mass = weight of trimmed hams, trimmed loins, plus trimmed shoulders; fat mass = weight of fat trimmed off from hams, loins, plus shoulders. Genotype x sex was included in the model independent of significance. Backwards elimination was used for modeling of other predictive terms ($P < .20$). For all animals with or without a record for final chemical body composition, average PD and LD during the experimental period were computed from predicted start and predicted final chemical body composition, start and final body weight, and the length of the experimental period.

There was considerable variation in start and final body weights of pigs belonging to the same weight range and feeding level (Table 2). In Appendix 1, it is described how this

Table 2. Least squares means of traits measured at the start, end or during the experiment for the three feeding levels per weight range[a]

Item[b]	Daily gain (g / d)	Daily feed intake (kg / d)	FCR[c] (kg / Kg)	PD (g / d)	LD (g / d)	Start weight (kg)	Final weight (kg)		Start backfat (mm)	Final backfat (mm)	
							T[d]	C[d]		T[d]	C[d]
25 – 65 kg											
- AL	835^{x}	1.65^{x}	1.99^{x}	129^{x}	157^{x}	27.1^{x}	68.5^{x}	69.6^{x}	-	9.5^{x}	9.6^{x}
- R1	620^{y}	1.25^{y}	2.03^{x}	97^{y}	90^{y}	25.8^{y}	64.8^{y}	65.8^{y}	-	8.4^{y}	8.5^{y}
- R2	466^{z}	1.00^{z}	2.19^{y}	77^{z}	51^{z}	26.0^{xy}	64.8^{y}	65.5^{y}	-	8.0^{z}	8.0^{y}
- RSD	86	.19	.22	12	31	5.5	6.9	5.6	-	1.1	1.1
65 – 95 kg											
- AL	919^{x}	2.37^{x}	2.64^{x}	135^{x}	313^{x}	68.9^{x}	99.3^{x}	99.7^{x}	8.6	11.7^{x}	11.7^{x}
- R1	677^{y}	1.79^{y}	2.72^{x}	106^{y}	194^{y}	66.2^{y}	97.3^{y}	97.7^{xy}	8.6	10.5^{y}	10.9^{x}
- R2	535^{z}	1.49^{z}	2.90^{y}	94^{z}	116^{z}	66.1^{y}	94.5^{z}	94.4^{y}	8.3	9.7^{z}	9.7^{y}
- RSD	119	.24	.45	24	70	10.6	8.1	8.0	1.4	2.0	2.0
95 – 125 kg											
- AL	786^{x}	2.50^{x}	3.31^{x}	115^{x}	203^{x}	93.1^{x}	126.6^{x}	128.1^{x}	10.2^{x}	14.8^{x}	14.5^{x}
- R1	612^{y}	1.92^{y}	3.31^{x}	99^{y}	120^{y}	89.8^{y}	123.4^{y}	124.9^{xy}	9.9^{xy}	12.5^{y}	12.7^{y}
- R2	420^{z}	1.51^{z}	3.76^{y}	74^{z}	67^{z}	88.6^{y}	120.3^{z}	121.1^{y}	9.7^{y}	11.5^{z}	11.7^{y}
- RSD	142	.28	.68	21	76	10.7	9.7	8.4	1.6	2.4	2.2

[a] Genotype and sex were included in the statistical model for each trait except for start and final weight.

[b] AL = ad libitum; R1 = restricted1; R2 = restricted2; RSD = residual standard deviation.

[c] FCR = feed conversion ratio.

[d] T = all animals; C = only animals that were analyzed chemically.

[x, y, z] within weight range and column item, lsmeans lacking a common superscript letter differ ($P < .05$).

variation was dealt with. In order to reduce effects of variation in body weight records on linear plateau model parameters, PD was adjusted linearly to PD for the target weight range. To estimate regression coefficients for start and final body weight needed for adjusting PD, a within weight range x feeding level regression of PD on start and final body weight was used:

$$PD = \beta_7 + G \times S + \beta_8 \text{ start body weight} + \beta_9 \text{ final body weight} + \text{Error} \qquad [3]$$

LD and daily feed intake were adjusted to LD and daily feed intake for the target weight range similarly.

Parameters of the linear plateau relationship were estimated for each combination of genotype, sex, and weight range. The relationship between PD and daily feed intake was obtained using a linear-plateau, broken-line model (NONLIN program (Sherrod, 1998); Möhn and De Lange, 1998):

PD = a1 + b1 x (daily feed intake – reference feed intake) [4a]

when daily feed intake was ≤ optimum feed intake and

PD = a1 + b1 x (optimum feed intake – reference feed intake) [4b]

leading to a constant PD when daily feed intake was > optimum feed intake.

Coefficient a1 represents the PD at the reference feed intake level. Reference feed intake was taken as 1.2, 1.6, and 1.7 kg / d for the weight ranges 25-65, 65-95, and 95-125 kg, respectively, representing a feed intake level in between restricted1 and restricted2 (Table 2). Coefficient a1 was expressed at these reference levels to reduce the mutual dependency of coefficients a1, b1, and optimum feed intake which enabled estimation of standard errors for the coefficients for almost each combination of genotype, sex, and weight range. The optimum feed intake, a1, and b1 were estimated by iteration until the RSD in the statistical model (4a and 4b) was minimized. The PD at the breakpoint was regarded as the maximum PD (PDmax). The estimate for optimum feed intake was used in the following model:

LD = a2 + b2 x (daily feed intake – optimum feed intake) [5a]

when daily feed intake was ≤ optimum feed intake and

LD = a2 + b3 x (daily feed intake – optimum feed intake) [5b]

when daily feed intake was > optimum feed intake.

Coefficient a2 represents the LD at optimum feed intake. The parameter estimates for a2, b2, and b3 were determined by iteration until the RSD in the statistical model (5a and 5b) was minimized. Regression coefficients b1 and b2 represent the increase in PD and LD per kg increase in daily feed intake at feed intake levels smaller than optimum feed intake. Coefficients b1 and b2 will be referred to as slope PD and slope LD. Ad libitum feed intake of pigs was used as an estimate for feed intake capacity.

Results

It can be derived from Table 2 that animals which were fed according to restricted1 and restricted2 actually received on average 75.8 and 60.6% (25-65 kg), 75.5 and 62.9%

Table 3. Linear-plateau model parameters and performance of ad libitum fed animals (± SE) per combination of genotype and sex for the weight range 25-65 kg

Genotype	Sex[a]	Linear part		PDmax[b]	FIopt[c]	Ad libitum performance			
		Slope PD (g / kg)	Slope LD (g / kg)	(g / d)	(kg / d)	Feed intake (kg / d)	Daily gain (g / d)	FCR[d] (kg / kg)	Final backfat (mm)
1	F	84[e]	151 ± 9	122	1.53[e]	1.47 ± .04	712 ± 14	2.08 ± .04	9.0 ± .2
	C	69 ± 10	99 ± 18	110	1.65 ± .09	1.69 ± .08	804 ± 27	2.09 ± .08	10.1 ± .4
	M	93 ± 12	174 ± 19	126	1.52 ± .08	1.43 ± .06	798 ± 19	1.79 ± .06	9.1 ± .3
2	F	109 ± 15	226 ± 36	131	1.44 ± .07	1.52 ± .08	795 ± 26	1.93 ± .08	8.8 ± .4
3	F	97 ± 6	215 ± 16	122	1.50 ± .03	1.53 ± .06	714 ± 21	2.16 ± .06	9.4 ± .3
4	F	79 ± 9	178 ± 18	144	1.73 ± .12	1.49 ± .07	798 ± 22	1.88 ± .07	8.4 ± .3
	C	121 ± 14	194 ± 14	135	1.49 ± .06	1.61 ± .07	853 ± 24	1.87 ± .08	9.1 ± .4
5	F	93 ± 13	151 ± 13	137	1.64 ± .10	1.62 ± .06	835 ± 20	1.97 ± .06	8.5 ± .3
	C	97 ± 6	115 ± 13	131	1.54 ± .03	1.67 ± .06	828 ± 21	2.01 ± .06	9.7 ± .3
Mean		94	167	129	1.56	1.56	793	1.98	9.1

[a] F = females; C = castrates, M = males.

[b] PDmax = estimated maximum PD capacity

[c] FIopt = estimated optimum feed intake capacity

[d] FCR = feed conversion ratio

[e] Standard errors could not be estimated due to mutually dependent parameters.

(65-95 kg), and 76.8 and 60.4% of ad libitum feed intake, respectively. This was close to the 75 and 60% level as aimed in the set up of the experiment. The difference in feed intake between the three levels was reflected in daily gain, final backfat thickness, PD and LD. Restricted2 fed animals had a higher feed conversion ratio than both other feeding levels. The average start weight of ad libitum fed animals was higher than start weight of restricted fed animals within each weight range.

In total, 1019 animals had estimates for PD, LD, and daily feed intake (Table 1), of which 309 were analyzed chemically (30%). Missing values for one or more of the three traits occurred incidentally as well as in clusters. Table 1 gives a good indication where missing values occurred as the number of pigs with data should be the same for the three feeding levels within a combination of genotype, sex, and weight range. Incidental missing values for PD and LD mainly occurred when an individual animal had a missing record for a post mortem trait that was used to predict the final chemical body composition or due to illness of the pig. Clusters of missing values for PD and LD occurred a few times when almost all animals slaughtered at one day had missing records of dissection results. In total, 34 ad libitum fed pigs (8.9% of all ad libitum fed animals) ended up without a record for average daily feed intake based on criteria derived by Eissen et al. (1999). Incidental and clusters of missing values for daily feed intake of ad

Table 4. Linear-plateau model parameters and performance of ad libitum fed animals (± SE) per combination of genotype and sex for the weight range 65-95 kg

Geno-type	Sex[a]	Linear part		PDmax[b]	FIopt[c]	Ad libitum performance			
		Slope PD (g / kg)	Slope LD (g / kg)	(g / d)	(kg / d)	Feed intake (kg / d)	Daily gain (g / d)	FCR[d] (kg / kg)	Final back-fat (mm)
1	F	50[e]	184 ± 33	-	-	1.97 ± .08	744 ± .27	2.72 ± .10	12.0 ± .5
	C	41 ± 13	337 ± 43	113	2.29 ± .28	2.47 ± .08	887 ± .24	2.81 ± .10	13.9 ± .5
	M	56[e]	208[e]	164	2.57[e]	2.07 ± .08	897 ± .26	2.24 ± .11	11.7 ± .5
2	F	85 ± 19	154 ± 76	135	2.01 ± .10	2.26 ± .08	978 ± .29	2.33 ± .11	11.3 ± .6
3	F	73 ± 25	112 ± 65	130	1.88 ± .14	2.36 ± .10	924 ± .36	2.59 ± .14	12.3 ± .7
4	F	61 ± 8	178 ± 29	130	2.03 ± .09	2.03 ± .07	793 ± .24	2.59 ± .10	9.4 ± .5
	C	41 ± 11	271 ± 53	136	2.48 ± .28	2.52 ± .08	930 ± .29	2.81 ± .11	10.5 ± .6
5	F	96 ± 15	268 ± 30	162	2.12 ± .11	2.16 ± .09	802 ± .32	2.75 ± .13	9.3 ± .6
	C	100 ± 18	215 ± 48	135	2.19 ± .12	2.74 ± .09	979 ± .31	2.83 ± .12	10.8 ± .6
Mean		67	214	138	2.20	2.29	882	2.63	11.2

\- No PDmax and FIopt were estimated.

[a, b, c, d, e] See footnotes Table 3

libitum fed animals occurred when the feed intake recording system had been functioning sub-optimally during the experimental period.

Linear plateau model parameters and feed intake capacity

Tables 3, 4, and 5 show the results for the linear plateau model parameter estimates and feed intake capacity for the three weight ranges, respectively. The performance of ad libitum fed pigs is included to provide general information about performance of genotypes and sexes. For two combinations of genotype, sex and weight range, no breakpoint could be estimated within the range of feed intake data, and consequently no optimum feed intake and PDmax were estimated. Mean slope PD was largest for the 25-65 kg and smallest for the 95-125 kg weight range. Mean slope LD increased from 25-65 kg to 65-95 kg, however, was smallest for the 95-125 kg weight range. Mean PDmax increased somewhat from 25-65 kg to 65-95 kg and was lowest within the 95-125 kg weight range.

Figure 2 shows the slope PD, PDmax, and feed intake capacity per weight range for respectively gilts (2a) and castrates (2b). Data of genotypes 1, 2, and 3 were pooled within dam line genotypes (indicated by D) and data of genotypes 4 and 5 were pooled within end product genotypes (indicated by E) to get a clearer picture of differences between genotypes, sexes, and weight ranges concerning PD. The length of each line indicates the data range concerning feed intake. The black squares represent the average actual feed intake of ad libitum fed animals (= feed intake capacity) per cluster of pigs. Some of the genotype / sex combinations had a feed intake capacity which was located almost in the

Table 5. Linear-plateau model parameters and performance of ad libitum fed animals (± SE) per combination of genotype and sex for the weight range 95-125 kg

Genotype	Sex[a]	Linear part		PDmax[b]	FIopt[c]	Ad libitum performance			
		Slope PD (g / kg)	Slope LD (g / kg)	(g / d)	(kg / d)	Feed intake (kg / d)	Daily gain (g / d)	FCR[d] (kg / kg)	Final backfat (mm)
1	F	39 ± 8	192 ± 60	89	2.35 ± .17	2.59 ± .15	733 ± 32	3.98 ± .18	16.7 ± .6
	C	20 ± 6	127 ± 20	74	2.41 ± .32	2.46 ± .15	532 ± 45	4.35 ± .19	17.7 ± .9
	M	79 ± 13	75 ± 52	163	2.36 ± .13	2.47 ± .10	733 ± 29	3.42 ± .12	15.4 ± .6
2	F	63 ± 18	127 ± 42	88	1.99 ± .12	2.11 ± .11	669 ± 32	3.38 ± .13	12.5 ± .6
3	F	65 ± 59	97 ± 70	69	1.79 ± .32	2.25 ± .15	528 ± 44	4.04 ± .18	14.9 ± .9
4	F	68 ± 11	231 ± 34	120	2.43 ± .15	2.36 ± .11	769 ± 31	3.17 ± .13	13.3 ± .6
	C	23 ± 7	99 ± 15	-	-	2.42 ± .13	676 ± 35	3.70 ± .16	13.6 ± .7
5	F	53 ± 9	139 ± 34	105	2.57 ± .17	2.51 ± .10	882 ± 30	2.98 ± .12	13.8 ± .6
	C	44 ± 8	121 ± 22	93	2.44 ± .19	2.40 ± .13	795 ± 34	3.42 ± .16	15.4 ± .7
Mean		49	134	100	2.29	2.40	702	3.60	14.8

\- No PDmax and FIopt were estimated.

[a, b, c, d, e] See footnotes Table 3

middle of the whole data range of feed intake. In that case, usually only one or two pigs had a feed intake capacity that was considerably larger than feed intake capacity of the other animals. For example only two end product castrates from 95-125 kg (Figure 2b) had a feed intake > 2.7 kg. For each weight range, PDmax was higher for end product than for dam line genotypes and higher for gilts than for castrates. PDmax of both lower weight ranges was especially constant for castrates (Figure 2b), whereas it increased somewhat with weight range for gilts (Figure 2a). PDmax of the highest weight range was lower than PDmax of both other weight ranges for each sex and cluster of genotypes. For end product genotypes, optimum feed intake increased with body weight. Feed intake capacity increased from 25-65 kg to 65-95 kg for gilts and castrates and both clusters of genotypes. From 65-95 kg to 95-125 kg, feed intake capacity was relatively constant for castrates and increased somewhat for gilts for both clusters of genotypes.

For 25-65 kg, average optimum feed intake equaled average feed intake capacity (1.56 kg / d) whereas for both other weight ranges average optimum feed intake was somewhat smaller than feed intake capacity (.1 kg; Tables 3-5). Figure 3 presents the optimum feed intake and feed intake capacity for each combination of genotype (1 to 5) and sex (F, C, and M) per weight range. For both lower weight ranges, feed intake capacity was higher for castrates than for gilts and boars. For the 95-125 kg weight range there was no clear sex effect on feed intake capacity (feed intake capacity of 4C was 2.4 kg / d). Data points below the diagonal line in Figure 3 represent combinations of genotype and sex that had a feed intake capacity insufficient to reach PDmax. Feed intake capacity was lower than optimum more often for gilts and boars than for castrates within genotype, and more often

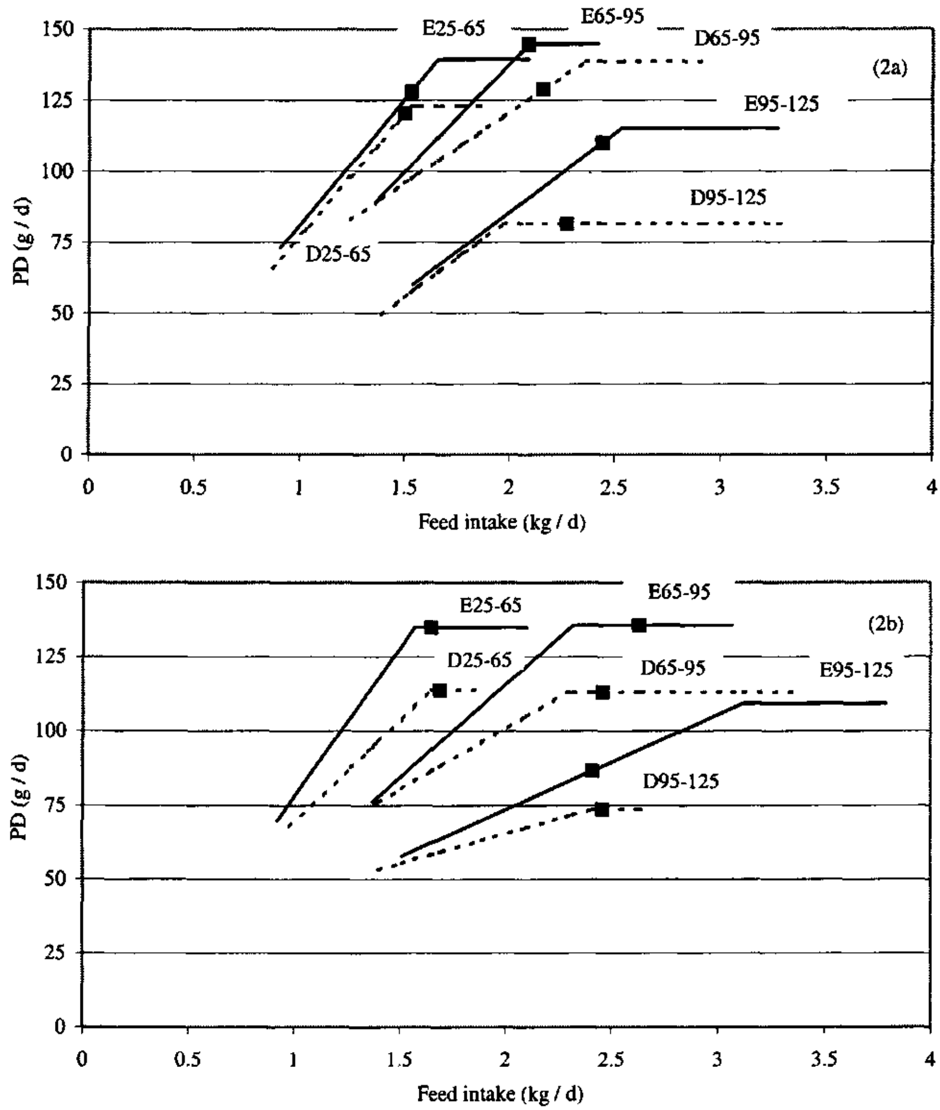

Figure 2. The relationship between PD and feed intake for dam line (D; dashed lines) and end product (E; solid lines) genotypes per weight range for gilts (2a) and castrates (2b). ■ represents the feed intake capacity.

for end product genotypes (genotype 4 and 5) than for dam line genotypes (genotypes 1-3). Differences between dam line and end product genotypes were particularly clear in the 95-125 kg weight range.

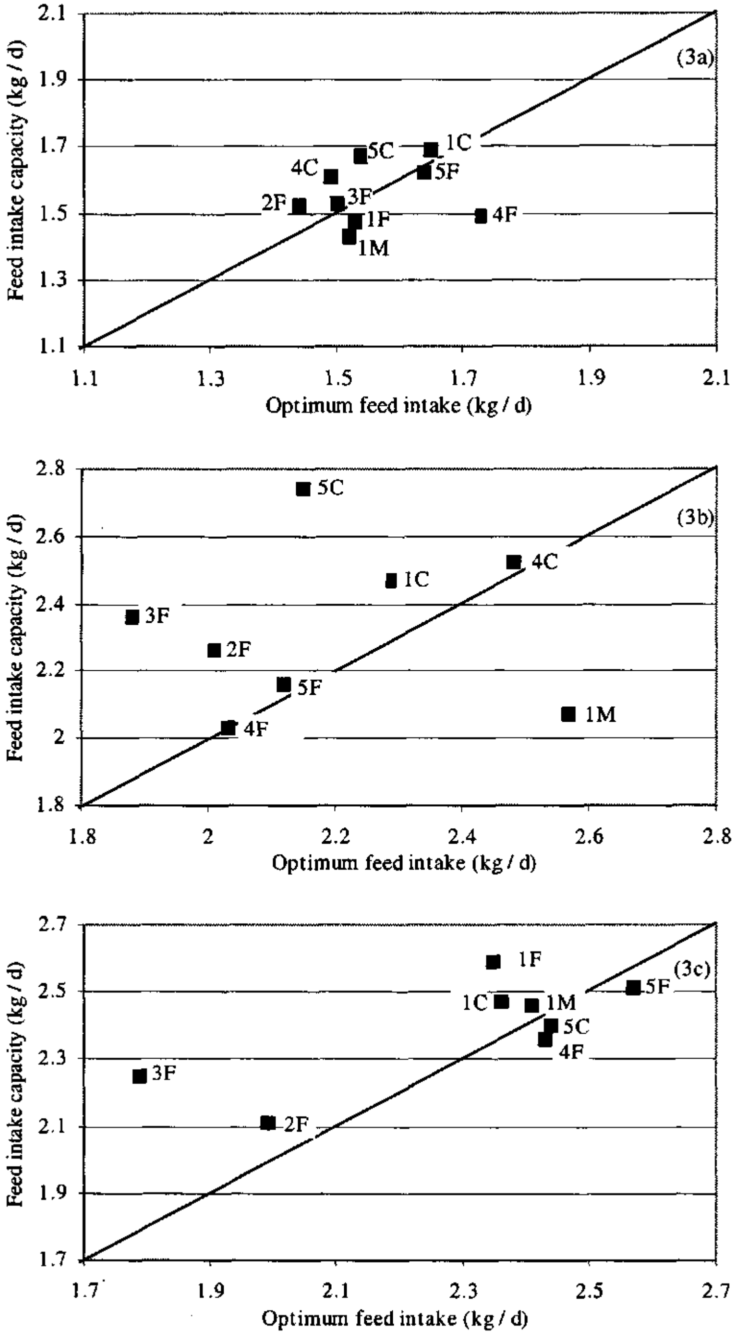

Figure 3. Feed intake capacity and optimum feed intake per combination of genotype (5 levels: 1, 2, 3, 4, 5) and sex (3 levels: females (F), castrates (C), males (M)) for the weight ranges 25-65 kg (3a), 65-95 kg (3b), and 95-125 kg (3c).

Discussion

In the present study, a biological model of the relationship between PD and feed intake was applied in order to derive selection directions for feed intake capacity of growing pigs. The growing period 25-125 kg was split into three weight ranges to study ad libitum feed intake in relation to optimum feed intake for the early, middle, and late phase of the growing period, separately.

In studies in literature that investigated effects of energy intake on PD or LD, pigs were housed in individual pens, whereas in practice pigs are housed in groups. In the present study, pigs were housed in groups. This resulted, however, in substantial variation in body weight within a pen and, as a consequence, in slaughter weight (Table 2). The variation in body weight due to within pen variation, and the sub-optimal connection between weight ranges (Table 2; Appendix 1) contributed to the substantial variation found in predicted start and final body composition. Inaccuracy in predicted chemical body composition caused variation in PD and LD estimates. This inaccuracy was ignored in the calculations of the linear plateau parameters. Presented standard errors for slope PD, slope LD, and optimum feed intake (Tables 3-5) should therefore be considered as minimum standard errors. General aspects of the data and methods used, which may have affected linear plateau model parameters or feed intake estimates which, however can not be quantified are described in Appendix 1.

Linear plateau concept parameters

In literature, slope PD decreases with body weight (De Greef, 1992; Quiniou et al., 1995; Bikker et al., 1996; Schinckel and De Lange, 1996), whereas slope LD increases with body weight (Bikker et al., 1996; Schinckel and De Lange, 1996). Present results for average slope PD (all three weight ranges) and slope LD (both lower ranges) were in line with these results. However, results for slope LD 95-125 kg were not. As a consequence of the lower slope LD 95-125 kg, the combined average increase in PD and LD per kg increase in feed intake (= slope PD + slope LD) was lower for the 95-125 weight range (183 g / kg) than for both other weight ranges (respectively 261 and 281 g / kg). Assuming that the deposition of 1 gram of protein (Van Es, 1979) and lipid (ARC, 1981) both cost about 53 kJ ME, independent of body weight, one would expect a combined deposition rate for 95-125 kg similar to both other weight ranges. Table 6 (Appendix 1) shows that start lipid percentage was significantly higher for ad libitum and restricted1 fed starting pigs than for slaughtered pigs at 95 kg which were used to predict the start lipid percentage. An overestimation of start lipid percentage results in an underestimation of

LD during the experimental period, which supports that slope LD 95-125 kg may be underestimated. The sum of slope PD and LD did not only differ over weight ranges but also over combinations of genotype and sex within each weight range (Tables 3-5). This suggests that biased or inaccurate prediction of start or final chemical body composition may also affect individual combinations of genotype, sex, and weight range.

Several studies investigated the effect of genotype and/or sex on slope and maximum level of protein deposition, indicating lower slopes and plateau levels in females and castrates compared with males, and lower slopes and plateau levels in unimproved compared with improved genotypes (Campbell and Taverner, 1988; Quiniou et al, 1995). Though results for slope PD per se (Tables 3-5) were not always in line with literature, Figure 2 showed that end product genotypes had a higher PD than dam line genotypes for any level of feed intake. Furthermore, gilts had in general a higher PD than castrates for any level of feed intake. The average PDmax was somewhat larger for the weight range 65-95 kg than for 25-65 kg, which is in line with literature that showed that PDmax is relatively constant between 25 and 90 kg of body weight (Whittemore and Fawcett, 1976; Quiniou et al., 1995; Möhn and De Lange, 1998). The lower average PDmax within 95-125 kg is also in line with literature (Thompson et al., 1996). The differences in PD between end product and dam line genotypes (Figure 2) were in line with expectations because genotype 2 and 3 sows were sired with boars that were selected for production traits to produce end product genotypes.

Ad libitum feed intake in relation to optimum feed intake

The present experiment was executed in a semi commercial environment using high quality commercial diets. These diets were used in order to realize a high daily energy intake of ad libitum fed pigs without the supply of amino acids, minerals, etc. being limiting for PD of restricted and ad libitum fed animals of any genotype or sex. Feed intake capacity was larger for castrates than for gilts for both lower weight ranges which is in agreement with literature (Kanis and Koops, 1990; Andersen and Pedersen, 1996). The absence of an effect of sex on feed intake capacity for 95-125 kg was unexpected and not in line with this literature. Furthermore, feed intake capacities of castrates from 65-95 kg and 95-125 kg were similar, whereas intake capacity of the higher weight range was expected to be higher (Kanis and Koops, 1990; Andersen and Pedersen, 1996). This suggests that feed intake capacity of castrates was underestimated from 95-125 kg. Possible causes may be the feed restriction during the pre-experimental period up to 95 kg, although one would expect rather an overestimation than an underestimation of intake capacity due to the pre-experimental treatment (see Appendix 1), and / or the composition of the diet. With regard to the latter, it is known that high protein levels in the diet may reduce the feed intake of animals (e.g., Cole and Chadd, 1989). Castrates may have suffered more from high levels of amino acids than the other sexes due to their lower PD levels.

The level of optimum feed intake should be studied in combination with the steepness of slope PD and the level of PDmax. The low level of optimum feed intake of gilts of genotypes 2 and 3 within each weight range was mainly the result of a relatively steep slope PD in combination with an average or somewhat lower than average level for PDmax (Table 3-5; Figure 3). The decrease in PDmax from 65-95 kg to 95-125 kg of body weight was somewhat larger for dam line than for end product genotypes (Figure 2). As a result, optimum feed intake did not increase from 65-95 kg to 95-125 kg for dam line genotypes, whereas it did increase for end product genotypes. There were no clear indications that one of the sexes (within genotype) had a higher or lower level of optimum feed intake than others. The observation that gilts had a feed intake capacity less than optimum more often than castrates favors the separate housing of sexes during the fattening period. In that case, diet composition and feed supply may be fit to the characteristics of each sex separately.

Within the 25-65 kg weight range, each combination of genotype and sex had a feed intake capacity close to optimum. This is in agreement with literature in which PDmax was not or just reached for animals lighter than 40–60 kg of body weight (Rao and McCracken, 1991; Bikker et al., 1995; Möhn and De Lange, 1996). In literature, the effect of body weight on linear plateau parameters has mainly been studied for body weights up to 95 kg, and no references were found for pigs up to 125 kg. Present results are in agreement with Kanis (1995) who showed, using simulation and assuming standard feed intake curves, that feed intake is too low to reach PDmax rather at the beginning or end than in the middle of the growing period.

For pig breeding companies it is important that end product genotypes have a feed intake capacity that is close to optimum. In present data set, feed intake capacity was around or below optimum for end product gilts for each weight range, whereas it was only limiting PD of castrates within 95-125 kg (Figures 2 and 3). However, none of the end product castrates had a feed intake capacity considerably larger than optimum, except for genotype 5 castrates within the 65-95 kg weight range. In general, it may be concluded that selection procedures as used by both breeding organizations over the last decades have not led to large discrepancy between ad libitum and optimum feed intake.

Implications

This study showed that the feed intake capacity of end product gilts is below or close to optimum during the growing period from 25-125 kg. It seems therefore beneficial to select for a higher ad libitum feed intake in combination with selection for other production traits. Moreover, it is recommended to house sexes separately during the growing period in order to feed animals optimally in balance with their characteristics.

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Appendix 1

Variation in start and final body weight in relation with prediction of body composition

There was substantial variation in start and final body weights of pigs (Table 2). Furthermore, Table 2 revealed that the connection between the three weight ranges was not always optimal. For example, average final weight of restricted1 fed animals that were analyzed chemically at 95 kg (i.e. data that were used to predict chemical body composition of starting animals at 95 kg) was 97.7 kg, whereas starting animals at 95 kg were, on average, considerably lighter (90.5 kg). This means that some extrapolation was necessary to predict start body composition at 95 kg. Data of genotypes and sexes were pooled to get more robust predictions of start and final body composition in order to deal with variation around start and final weights (models 1 and 2). It was assumed that pooling of data would not introduce bias in PD or LD estimates. To study effects of pooling data on PD and LD for genotypes and sexes, a second estimate for PD and LD was computed for animals that were analyzed chemically after slaughter. For the second estimate of PD and LD, recorded instead of predicted final chemical body composition was used. On average, differences were small between both estimates for PD and LD and pooling of data did not cause systematic under or overestimation of PD or LD for certain genotypes or sexes. Therefore, it is assumed that pooling in general has not introduced bias in PD or LD estimates.

General aspects of the data and methods used

It was studied whether the data that were used to predict chemical body composition at the start were representative for starting animals. Table 6 presents the results for predicted chemical body composition of animals that start the experiment (starting animals) and of animals that were used to develop prediction formulas for the composition of these starting animals (slaughtered animals). Lipid percentage of the slaughtered animals differed ($P < .05$) from ad libitum (65 and 95 kg) and restricted1 (95 kg) fed starting animals. Furthermore, protein percentage tended to be higher for slaughtered animals than for ad libitum fed starting animals ($P < .10$) at 65 kg. There were no differences in chemical body composition ($P > .10$) between the three feeding levels of starting animals which reflects that littermates were randomly assigned to the three feeding levels.

The relative importance of bias in start body composition (Table 6) on PD and LD depends on the ratio between length of the experiment (kg) and absolute start body weight (Black, 1995), the importance being higher when the ratio is lower. Therefore, bias in start body composition will affect the weight range 25-65 kg least and 95-125 kg most. Bias in

Table 6. Least squares means for predicted chemical body composition at 25, 65 and 95 kg per group of animals[a]

Group	Body weight (kg)					
	25		65		95	
	Protein %	Lipid %	Protein %	Lipid %	Protein %	Lipid %
Slaughtered animals[b]	14.82	11.28	15.57	13.51^{y}	15.70	17.60^{y}
Starting animals						
- Ad libitum	14.85	11.28	15.39	13.12^{z}	15.67	18.28^{z}
- Restricted1	14.84	11.28	15.44	13.25^{yz}	15.66	18.24^{z}
- Restricted2	14.84	11.28	15.44	13.28^{yz}	15.71	18.02^{yz}
RSD[c]	.12	.25	.51	.81	.42	1.63

[a] Genotype and sex were included in the statistical model as class variables; body weight was included as a continuous variable.

[b] Predicted chemical body composition of slaughtered animals that were used to predict the chemical body composition of starting animals at the same level of body weight.

[c] RSD = residual standard deviation.

[y, z] Within a column, groups lacking a common subscript letter differ ($P < .05$)

start body composition will result in an underestimation or overestimation of protein and lipid weight at he start (kg) and, consequently, in an underestimation or overestimation of PD and LD. Within each weight range, the absolute bias in PD and LD estimates is largest in ad libitum, and smallest in restricted2 fed pigs as length of experimental period reduces the absolute bias.

It was not possible to correct for differences in year-season such that effects of genotype and sex could adequately be disentangled from year-season effects. Therefore, year-season was not included in any of the analysis.

The nutritional history of pigs during the pre-experimental period may affect the realized PD and LD (Quiniou et al., 1995; Bikker et al., 1996; Möhn and De Lange, 1998), and therefore linear plateau model parameters. Exposure to an energy intake restriction after a period of a higher feeding level may result in a reduced need to deposit essential body lipid, rendering more energy available for PD (Möhn and De Lange, 1998). Therefore, PD of restricted1 (25-65 kg) and restricted2 (all weight ranges) fed animals may have been overestimated and LD underestimated during especially the first week(s) after starting the experiment. On the other hand, ad libitum fed animals starting at 65 or 95 kg, which were fed according to restricted1 from 25 kg onwards, may have shown compensatory effects (Bikker et al., 1996), which may have resulted in an overestimation of PD and feed intake capacity. Compensatory feed intake likely contributed to the higher live body weight recordings of ad libitum fed animals compared with restricted fed animals at the start of each weight range after the 3-4 d adaptation period (Table 2).

Restricted1 and restricted2 fed animals received on average about 75 and 60% of the amount of feed eaten by ad libitum fed animals. Slope PD was based on PD data of restricted and ad libitum fed animals, whereas PDmax was predominantly based on ad libitum fed animals. Animals with the largest ad libitum feed intake had a relatively large effect on PDmax, especially when only a few animals had a feed intake record larger than the estimated optimum feed intake. Kanis (1990) showed that animals with a large feed intake capacity grow somewhat fatter than animals with a smaller feed intake capacity when fed restricted on a fixed amount of feed. As a consequence of the method used, PDmax, and as a result optimum feed intake, may have been underestimated, especially when the PDmax estimate was based on only few animals.

6 Sow Factors Affecting Voluntary Feed Intake during Lactation

Genetic and environmental changes during the last few decades have resulted in higher milk production and maintenance costs of lactating sows, leading to increased energy requirements, whereas the amount of body fat reserves of, in particular, young immature sows have decreased and voluntary feed intake may have decreased. As a consequence, present voluntary feed intake of sows during lactation is frequently inadequate to meet nutrient demands. This may influence subsequent reproduction. In this paper, it is argued that voluntary feed intake of lactating sows should be included in breeding programs. To underpin this statement, it is reviewed how the sow factors body weight and body composition at farrowing, litter size during lactation, parity and genotype affect voluntary intake during lactation and possible physiological mechanisms are provided. It is concluded that, for sustainable pig production, the trends of decreasing fat reserves at farrowing and increasing energy requirements during lactation should be accompanied by a higher feed intake capacity during lactation. Genotype seems the most appropriate sow factor that can be used to realize the desired changes and selection for a higher voluntary feed intake during lactation is recommended.
Keywords: Body composition, Feed intake, Genotype, Lactation, Litter size, Parity, Sows

Introduction

Voluntary feed intake of young and immature sows during lactation is frequently inadequate to meet nutrient demands for maintenance, milk production and body growth (Noblet et al., 1990). Milk production has a high priority and, if nutrient intake is insufficient, the sow will mobilize body tissue in an attempt to maintain milk production (NRC, 1987). Recent work cited below illustrates that nowadays nutrition is more critical for reproduction than in the past. For example, earlier work of Elsley et al. (1969) and O'Grady et al. (1973) clearly indicated no relationship between lactational feed intake and subsequent reproduction performance. In recent studies, however, a low feed intake during lactation, accompanied by excessive weight loss, was found to be associated with

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several common reproductive problems, including an increased interval from weaning to estrous (Reese et al., 1982; King and Williams, 1984; Kirkwood et al., 1987a, 1987b, 1990; Baidoo et al., 1992), an increased incidence of anestrus (Kirkwood et al., 1987a, 1987b), a lower ovulation rate (Zak et al. 1997), a decreased conception rate (Kirkwood et al., 1987a, 1987b) and a higher embryonic mortality (Kirkwood et al., 1987a, 1990; Baidoo et al., 1992). The longer length of lactation in the earlier works may have contributed to the lower sensitivity of sows in the past, because sows mainly loose body reserves during the first 2-3 weeks of lactation and start to recover afterwards (Revell and Williams, 1993). All of the above-mentioned studies restricted feed intake during at least part of the lactation in controlled experiments. However, data analyses of (close to) ad libitum fed sows on commercial farms also show that a higher feed intake during lactation may improve reproductive performance (Koketsu et al., 1996b, 1997; Koketsu and Dial, 1997).

According to Whittemore (1996), this turn of events may have resulted from a change in the pig's genetic make-up. In dam lines, selection has generally been for production and reproduction traits. Selection for production traits has resulted in an increase in growth rate, a reduction in backfat and an improved feed efficiency during the growth phase (e.g., Vangen and Kollstad, 1986). These changes during the growth phase are reflected at later stages in a reduction in the amount of fat in the body of young sows at the times of parturition and weaning (Whittemore, 1996). Furthermore, maintenance requirements at maturity are higher due to a higher mature body weight. Sows also have higher maintenance requirements due to the lower fatness (Campbell and Taverner, 1988). The common breeding objective for reproduction focuses on the number of piglets weaned per sow per year (Knap, 1990). The effect of selection for reproduction traits is illustrated by the positive genetic trends for litter size in current dam lines (Knap et al., 1993). Litter size also tends to increase due to environmental improvements (Southwood and Kennedy, 1991). As a result of indirect selection, increased litter size and / or improvement of the environment, milk production of sows also increased over recent decades (Whittemore, 1996; Mackenzie and Revell, 1998).

Though selection may not have been directly for voluntary feed intake of pigs or sows, there are clear illustrations that selection for production traits may affect voluntary feed intake. Breeding programs putting a high emphasis on production efficiency or leanness rather than on rate of lean growth, can reduce the appetite of growing pigs (Smith and Fowler, 1978; Ellis et al., 1979; Ellis et al., 1983; Smith et al., 1991). A reduction in appetite during the growth phase can also be reflected by sows during lactation (Kerr and Cameron, 1996b).

Many factors affect spontaneous feed intake during lactation. For convenience they can be grouped under three main headings, although some of them interact with each other (Revell and Williams, 1993). The three factors are sow (e.g., body weight and composition, litter size, parity, genotype), environment (e.g., temperature, air quality, management, length of lactation, stock density, disease incidence) and diet (e.g., digestibility, composition, energy density, protein and amino acid balance, availability of water, feeding frequency). As indicated above, current selection strategies result in increasing energy requirements of sows due to higher milk production and maintenance costs, whereas the amount of fat reserves of young sows is decreasing and voluntary feed intake may be decreasing. Nowadays, inadequate feed intake during lactation is particularly evident in primiparous sows (NRC, 1987), sows fed generously during gestation (Baker et al., 1968; Dourmad, 1991) and sows in a hot environment (NRC, 1987). Therefore, it can be argued that voluntary feed intake during lactation should be considered in breeding programs. The aim of this paper is to review and provide possible physiological mechanisms for the way in which the mentioned sow factors affect voluntary feed intake during lactation and to investigate if selection for feed intake during lactation should be recommended.

Voluntary feed intake

Control of voluntary feed intake in general

The control of feed intake and regulation of energy and protein balance are influenced by a large number of factors. In the past various theories of intake control have been put forward, for example, based on blood glucose levels (glucostatic regulation; Mayer, 1953), body fatness (lipostatic regulation; Kennedy, 1953) or on a constant body temperature (thermostatic control; Brobeck, 1948). Nowadays, the various theories are no longer considered as alternatives but rather as complementary to each other; together they contribute to a multifactorial control system (Forbes, 1988).

The control of feed intake is extremely complex and involves central as well as peripheral mechanisms. The primary site responsible for the integrated control of feed intake and energy balance is the central nervous system (CNS), although the specific mechanisms involved are not well understood (NRC, 1987). Peptides found in the CNS have been shown to have a direct effect on the control of metabolism and feed intake. For instance, the onset of feeding may be affected by opioid peptides, whereas termination of feeding may involve cholecystokinin. A number of CNS centers and, most likely, peripheral receptor systems exist that provide information about the animal's metabolic

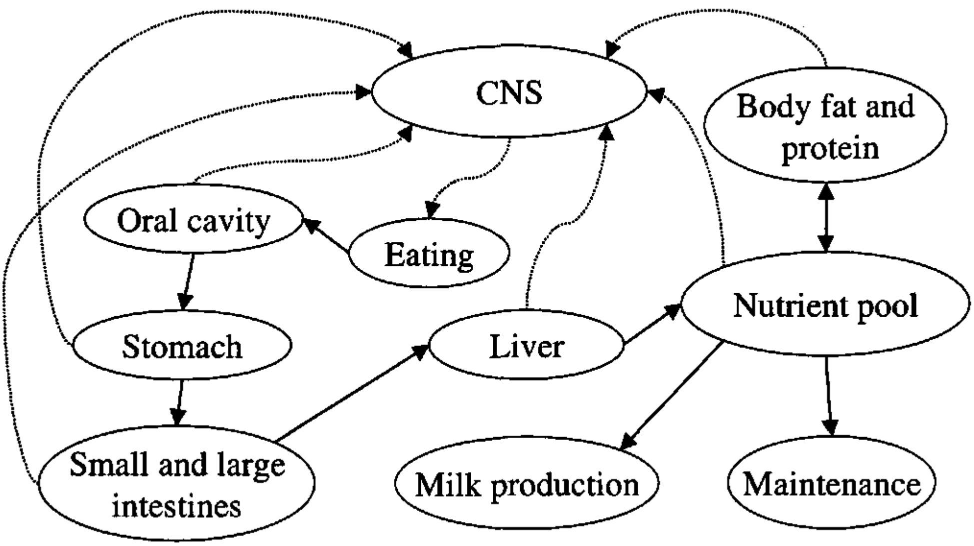

Figure 1. Schematic diagram of a general model of feed intake regulation of a lactating sow. Solid arrows represent flows of nutrients whereas dashed arrows represent information signals regulating feed intake.

state. A coordinated feeding behavior is established via these receptor systems and CNS centers (NRC, 1987).

Figure 1 shows a diagram of a plain general model of feed intake regulation of a lactating sow. Stimuli that modulate feeding behavior act at the pre-absorptive (physical regulation) and / or post-absorptive (metabolic regulation) level. The oral cavity, stomach and small intestine are the pre-absorptive sites of action of these stimuli, whereas the liver and brain appear to be the post-absorptive sites (Scharrer, 1991; Tybirk, 1989). At the pre-absorptive level, feed intake is regulated by mechano-, chemo- and osmoreceptors and by release of hormones, e.g., cholecystokinin (Scharrer, 1991). Stomach distension is signaled to the brain through vagal afferents (Gonzales and Deutsch, 1981), whereas humoral and nervous signals inform the brain about the presence of nutrients in the small intestinal lumen (Stephens, 1985). At the post-absorptive level, circulating nutrients in the blood are important and liver, brain and body reserves seem to be involved in the regulation of feed intake (Scharrer, 1991).

Long-term versus short-term regulation

Voluntary feed intake is regulated at two levels (Revell and Williams, 1993). The first is short-term regulation, which involves the factors regulating meal eating behavior, i.e., meal size and meal length. The second is long-term regulation, which determines the average daily intake over a period of time. The daily feed intake of an animal is the summation of intake during individual meals. While meal size can vary greatly, the total quantity eaten each day, for example, must be controlled to maintain energy homeostasis. The signals of satiety that control meal size must have shorter time constants than the signals that regulate long-term energy balance (NRC, 1987). If animals are confronted with periodic feed-associated stimuli, variable feed availability, changing social situations or novel stimuli, they readily modify their eating pattern while maintaining long term energy homeostasis (Woods et al., 1998).

Signals from the gastrointestinal tract are likely to be of major importance in the short-term control of voluntary feed intake since feed ingestion ceases before the meal has been completely digested and absorbed (Rayner and Gregory, 1989). The size of each meal appears to be regulated by rapidly acting negative feedback controls initiated by the presence of feed in the gastrointestinal tract involving a quick qualitative and quantitative evaluation of the feed (Houpt, 1984; Le Magnen and Devos, 1984; Forbes, 1988). The products of a meal (nutrients) can be more accurately monitored after the meal (postprandial) and used to determine the onset of the next meal. Meal to meal intervals, and therefore meal frequency, mainly depend on post-absorptive factors (Le Magnen and Devos, 1984; Forbes, 1988). Long-term control may also involve the gastrointestinal tract, but metabolic factors are likely to be more important (Rayner and Gregory, 1989).

Stricker and McCann (1985; cited by Forbes, 1988) summarized meal eating behavior in relation with short and long term regulation as follows: 'during eating, both increasing gastric fill and increasing hepatic delivery of calories serve to reduce the likelihood that animals continue to feed. Once they stop eating, they will remain satiated despite an empty stomach so long as the liver continues to get utilizable calories from the intestines'.

Lactating sows

Lactation feed intake is low immediately post farrowing and increases as lactation proceeds, reaching a maximum in the second or third week (Koketsu et al., 1996a). It is usually recommended to restrict feed intake during the first days of lactation, especially to support adaptation to new lactation feeds and to reduce occurrence of post partum agalactia (Neil, 1996; Noblet et al., 1998). The pattern of voluntary feed intake during lactation is related to that of milk production as at least 70% of the total of a sow's lactation energy requirement is needed to support lactation (Aherne and Williams, 1992). Calculations presented by Revell and Williams (1993) suggest that sows loose body reserves during the first two to three weeks of lactation to support milk production. Thereafter, sows start to recover; however, the remaining one to two weeks of a normal four-week lactation is generally too short to compensate completely for the losses during the first two to three weeks.

Lactation brings about a large increase in feed intake compared with gestation feed intake. Lactating sows may support this by eating more meals and / or larger and longer meals during lactation (Dourmad, 1993; Weldon et al., 1994a). During early lactation, voluntary feed intake may be reduced due to gastro-intestinal limitations, as the gastro-intestinal tract may need time to adapt to the new situation of high daily feed intake (Dourmad, 1991). The latter is supported by results of Farmer et al. (1996) who showed that, at similar gestation energy intakes, voluntary feed intake during lactation was higher in sows receiving higher feeding levels during gestation from low energy diets. It is also supported by the observation that voluntary feed intake was independent of daily feeding frequency of lactating sows (NCR-89, 1990) and ewes (Revell and Williams, 1993); however the ewes needed a few days to adjust to the new situation. Results presented by Owen and Ridgman (1967, 1968) who fed growing pigs diets that were diluted with varying amounts of sawdust, illustrate a similar effect. The animals were able to increase their feed intake as the proportion of sawdust in the diet increased but this compensation was not immediate (i.e., more than one week) and not sufficient to maintain energy intake (Revell and Williams, 1993). It may be important that compensation in feed intake in the long-term is not complete; hence, factors that are normally considered as short-term regulators may have effect in the long-term but at a diminished level (Revell and Williams, 1993).

Temperature has a large effect on feed intake. The situation in the farrowing room is complicated since suckling piglets have higher temperature requirements than the lactating sow. The upper limit of the zone of thermal comfort (i.e., above the evaporative critical temperature) is around 22 °C for the sow, whereas the lower limit is around 30 °C for suckling piglets (Black et al., 1993). When the environmental temperature rises above the evaporative critical temperature of the sow, the sow can only control body temperature by increasing heat loss through evaporation or by reducing its heat production by eating less (Williams, 1998). Black et al. (1993) and Messias de Bragança et al. (1998) found a decrease in voluntary feed intake of 40 and 43% in lactating sows when the temperature was raised from 18 to 28 °C and 20 to 30 °C, respectively. The reduced voluntary feed intake may partly be due to a lower milk production at higher temperatures. Black et al. (1993) suggested that blood flow is redirected to the skin in case of high environmental temperatures to increase heat losses, at the expense of blood flow to the mammary gland and other organs. Nutrients would then be diverted from the mammary gland. This hypothesis is supported by Messias de Bragança et al. (1998), who showed that sows kept at 20 °C and fed a similar amount of feed as ad libitum fed sows kept at 30 °C had a numerically and significantly higher litter weight gain during the first two weeks and third week of lactation, respectively.

Sow factors

The interrelationships between milk production, changes in body weight and composition, and voluntary feed intake during lactation (Figure 1) are complex and the controls of partitioning of nutrients between milk secretion and deposition or mobilization of body reserves are poorly understood. The physiological drive of lactating sows to produce milk at the expense of other body functions is, however, a key component of the metabolic state of lactating sows and is controlled by factors like litter size, parity and genotype (Pettigrew et al., 1993). It will be discussed below how the sow factors body weight and body composition at farrowing, parity, litter size and genotype may affect voluntary feed intake of lactating sows.

Body weight and body composition at farrowing

Because feed intake during early lactation is generally too low to meet the energy requirements, high producing sows mobilize body reserves to supply energy and nutrients for milk production and hence to maintain and stimulate the growth rate of piglets (Mullan and Williams, 1989). When sows are allowed a high feeding level or ad libitum access to feed during gestation, they consume more feed than needed to meet their energy requirement during gestation. Sows fed a high gestation feeding level, however, have a lower voluntary feed intake during lactation than sows fed according to their requirements during gestation, and mobilize more reserves during lactation (e.g., Mullan and Williams, 1989; Yang et al., 1989; Dourmad, 1991; Weldon et al., 1994a; Xue et al., 1997; Revell et al., 1998a; Figure 2). Le Cozler et al. (1998a) showed that a higher feeding level during rearing (ad libitum vs 80% of ad libitum) also led to a lower voluntary feed intake during lactation (Figure 2). Points are connected per study in Figure 2 to indicate that each study shows an effect of a similar magnitude.

A higher feeding level during rearing and / or gestation generally results in a higher body weight and body fatness of sows at farrowing. The higher body fatness at farrowing seems to be associated with the lower lactation feed intake (Dourmad, 1991; Williams and Smits, 1991; Revell et al., 1998a), whereas the effect of body weight at farrowing seems to be small (O'Grady et al., 1985; Williams and Smits, 1991; Weldon et al., 1994a). The

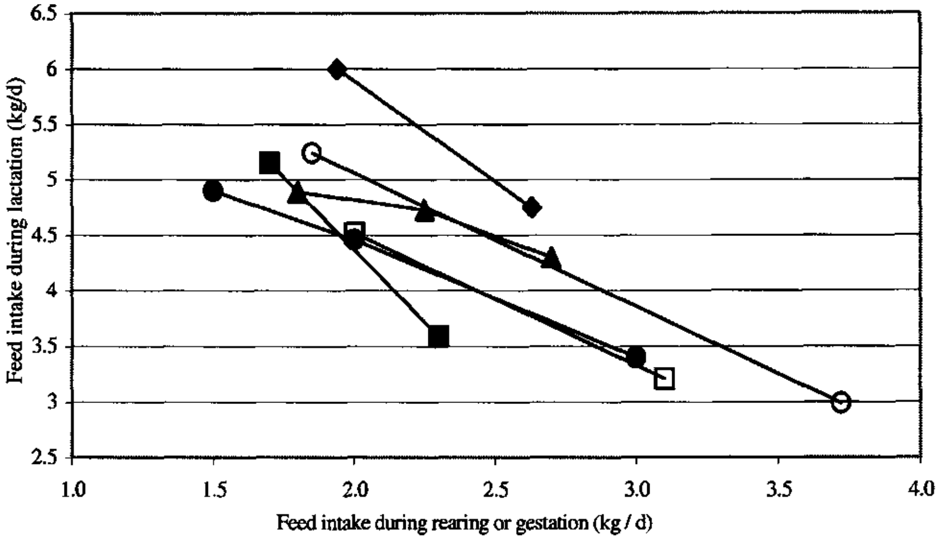

Figure 2. Relationship between daily feed intake during rearing (◆) or gestation (other symbols) and voluntary feed intake during lactation of a sow: ■ Revell et al. (1998a); ● Mullan and Williams (1989); ▲ Dourmad (1991); ◆ Le Cozler et al. (1998a); □ Xue et al. (1997); O Weldon et al. (1994a).

effect of body fatness was illustrated by regression analyses of daily feed intake during lactation on backfat thickness at farrowing: Yang et al. (1989) estimated a slope of –18 and –129 g d^{-1} mm^{-1} for primiparous and multiparous sows, respectively, Dourmad (1991) estimated a slope of –63 g d^{-1} mm^{-1} for primiparous sows and Koketsu et al. (1996a) estimated a slope of –19 g d^{-1} mm^{-1} across all parities.

Body weight and fat depots influence feed intake presumably by modulation of long-term regulation mechanisms. The various control mechanisms are either independently unique in action or synergistic and may vary according to the phase of the lactation period. How these may interact remains to be elucidated. Several studies focussed on one or two of the mechanisms. Most of these studies used different, usually two, feeding levels during rearing or gestation resulting in relatively fat and lean sows at farrowing. During lactation all sows were fed ad libitum. Mechanisms possibly explaining the effect of body composition on lactation feed intake of sows are turnover of body fat tissue, insulin and leptin levels in blood and cerebrospinal fluid, presence of insulin resistance and glucose intolerance, and levels of milk production and body protein reserves. These five mechanisms are described below, followed by paragraphs about meal eating behavior of fat and lean sows, the effect of body fatness on voluntary lactation feed intake in relation to stage of lactation, and optimum body composition of sows at farrowing.

Turnover of body fat tissue

Firstly, fat is stored in the body with a continuous turnover which involves the release of fatty acids and glycerol (Forbes, 1988). The release into the bloodstream is greater when the amount of body fat is greater. The concentrations of mentioned substrates or the extent of oxidation may act as signals that could be read by the liver and sent to the brain via vagal nerves (Williams, 1998). Therefore, the sow may use the rate of fat metabolism to regulate and monitor its energy status and hence voluntary feed intake (Williams, 1998). Glycerol may be a better indicator of body fatness than nonesterified fatty acids (NEFA) because the only source of plasma glycerol is from the breakdown of triacylglycerides (Revell et al., 1998a). Moreover, almost all glycerol from the breakdown of triacylglycerides is released directly into the blood circulation and very little glycerol is reesterified into triacylglycerides in adipose cells. Nonesterified fatty acids, on the other hand, may be reesterified into triacylglycerides to a larger extent than glycerol before leaving adipocytes (Revell et al., 1998a). Levels of NEFA are therefore better indicators for fat mobilization than for body fatness per se.

Concentrations in blood of NEFA during late gestation were not significantly affected by rearing or gestation feeding level (Weldon et al., 1994a; Revell et al., 1998a; Le Cozler et al., 1998b). Levels of glycerol, however, were significantly higher in fat sows, which supports the mechanism described above (Revell et al., 1998a). During the first weeks of lactation, levels of NEFA and glycerol were always higher in fat than lean sows (Weldon et al., 1994a; 1994b; Revell et al., 1998a; Le Cozler et al., 1998b). However, it is not clear whether these higher levels found post partum in fat sows cause, or are a consequence of, the lower feed intake of fat sows, involving another mechanism.

Insulin and leptin

As animals fatten, there is a gradual increase in basal blood insulin (Woods et al., 1985, 1998) and leptin concentrations (Woods et al., 1998). Concentrations in the blood are the difference between release in the blood and breakdown or uptake. Basal insulin is defined as the amount of insulin measurable in the blood in the absence of exogenous influences such as feed. It is generally estimated after a fast of 12-24 h. Insulin secretion is stimulated acutely in response to the intake of a meal, whereas leptin secretion is not. The mechanisms governing leptin secretion remain to be elucidated, but insulin appears to play a key role (Woods et al., 1998). Insulin is secreted from pancreatic beta cells, whereas leptin is a product of the obese gene which is expressed only in fat tissue. It is known that insulin and leptin from the blood can penetrate into the cerebrospinal fluid at a slow rate, and that levels within the cerebrospinal fluid can be considered as an indicator over time of the levels in the blood (Woods et al., 1985, 1998). Cerebrospinal fluid levels change relatively slow and thus are a more stable parameter than blood levels. Higher levels of blood insulin and leptin as a result of a high feeding level during gestation would, therefore, lead to higher levels of both in cerebrospinal fluid at farrowing, which may inhibit feed intake (Woods et al., 1998; Williams, 1998). Insulin and leptin then would act as a homeostatic mechanism for body fat at the brain level.

No references were found in which concentrations of leptin and insulin in the cerebrospinal fluid or concentrations of leptin in blood of fat and lean sows were measured. Xue et al. (1997), Revell et al. (1998a) and Le Cozler et al. (1998b) collected blood samples during late gestation after fasting and found no difference in basal insulin levels between fat and lean sows. Weldon et al. (1994b) reported no effect of gestation feeding level on basal insulin level on day 1 of lactation. Basal insulin level at day 15 of lactation was even lower for the high gestation feeding level group (Xue et al., 1997).

These results suggest that the contrast between lean and fat sows was not large enough to find differences in basal insulin levels or that differences are more likely to be measured in cerebrospinal fluid (Revell et al., 1998a).

Insulin resistance and glucose intolerance

Another possible mechanism that also involves insulin is the development of insulin resistance and / or glucose intolerance. Insulin usually regulates both blood glucose levels and fat mobilization, with the result that oxidation of NEFA is depressed and oxidation of blood glucose is stimulated (Kronfield, 1971; Revell and Williams, 1993). Excessive feed intake during gestation may cause the sow to become insensitive to insulin, probably by affecting insulin receptor number and / or affinity. The sow will then exhibit a smaller response in glucose clearance to the same amount of insulin (Weldon et al., 1994b). A high feeding level during gestation may also cause the sows to become glucose intolerant, possibly by decreasing the number of glucose receptors and reducing sensitivity of beta-cells in the pancreas to glucose (Murray et al., 1990; cited by Xue et al., 1997). When a sow becomes glucose intolerant, she will exhibit a smaller response in blood insulin to the same amount of glucose (Xue et al. 1997). Both insulin resistance and glucose intolerance may lead to higher glucose concentrations after a meal.

Development of insulin resistance and / or glucose intolerance presumably results in a lower clearance rate of glucose from the blood after a meal. As a consequence, use of peripheral glucose is likely decreased and voluntary feed intake may be reduced to maintain blood glucose concentrations. Furthermore, lower blood insulin levels as a result of glucose intolerance may enhance the mobilization and oxidation of stored adipose tissue as oxidation of NEFA is depressed to a lesser degree. The latter also may reduce voluntary feed intake.

In a number of studies, sows were fed according to a normal or high feeding level during gestation resulting in relatively lean and fat sows, and blood glucose and / or insulin levels in late gestation and / or lactation were determined, usually after an overnight of fast and after infusion of glucose. During late gestation, Xue et al. (1997) found fat sows to be more glucose intolerant, illustrated by higher glucose and lower insulin concentrations in fat sows after glucose infusion compared with lean sows. Revell et al. (1998a) did not find differences between fat and lean sows in late gestation after glucose infusion. At day1 of lactation, Weldon et al. (1994b) found symptoms of insulin resistance as insulin peak secretion after glucose infusion was not affected by gestation feeding level, but the rate at which glucose was cleared from the blood was much slower for the fat sows. Xue et al. (1997) infused sows with glucose at d15 of lactation and again found fat sows to be more glucose intolerant, the impaired glucose tolerance being more severe during lactation than during late gestation. Weldon et al. (1994a) and Revell et al. (1998a) studied blood glucose and insulin concentrations during lactation without infusing glucose. Weldon et al. (1994a) found lower concentrations of insulin for fat sows, whereas concentrations of glucose were not influenced, which also points towards glucose intolerance. Differences in insulin levels were especially clear during early lactation. Revell et al. (1998a) did not find an effect of gestation feeding level on glucose or insulin concentrations during mid and late lactation.

Le Cozler et al. (1998b) varied the feeding level during rearing, while all sows received the same amount of feed during gestation. The difference between fat and lean sows at farrowing was therefore mainly a carry over effect from the rearing period. Infusion of sows with glucose in late gestation did not affect rate of glucose clearance; however, a higher peak insulin secretion was observed for fat sows, showing that fat sows may be more resistant to insulin. During mid lactation, fat sows showed a poorer glucose tolerance and appeared to be more resistant to insulin than lean sows after glucose infusion. It seems, therefore, that impaired glucose clearance is more likely caused by body composition at farrowing per se, than by a high feeding level during the preceding gestation.

In conclusion, it seems that differences in glucose intolerance and insulin resistance between fat and lean sows may, at least partly, explain the lower voluntary lactation feed intake of fat sows, although results are not fully unambiguous. Results of the studies in which glucose was infused may differ due to the dose used, as Weldon et al. (1994b) and

Xue et al. (1997) infused 1 g glucose per kg body weight, whereas Revell et al. (1998a) and Le Cozler (1998b) infused .06 g and .5 g per kg body weight, respectively.

Milk production

Head et al. (1991) and Head and Williams (1991) reported that fat sows, in comparison with lean sows, had a lower capacity to secrete energy in milk because they had fewer milk secretory cells. This may have caused the significantly reduced litter growth of the fat sows reported by Head and Williams (1995). Revell et al. (1998b) reported that milk yield was about 15% higher in lean than fat sows, which was also reflected in litter growth. A lower milk production may diminish the drive to eat and reduce voluntary feed intake of sows (Figure 1). In most other studies, however, litter growth was not affected by a high gestation feeding level and fatness at farrowing, indicating that the effect of fewer milk secretory cells of fat sows was probably limited (e.g., Dourmad, 1991; Weldon et al, 1994a; 1994b; Xue et al., 1997).

In dairy cattle, rapid rates of growth in the prepubertal period are associated with substantial reductions in milk production in all subsequent lactations (Little and Kay, 1979; Sejrsen et al., 1982). Recent reports suggest that the deleterious effect is associated with feeding heifers a diet with an inadequate protein:energy balance resulting in an excessive fat deposition during the prepubertal period (Mackenzie and Revell, 1998). Gilts may be similarly affected during gestation, which is supported by the fact that Head et al. (1991), Head and Williams (1991, 1995) and Revell et al. (1998b) used suboptimal diets during gestation in order to support fat deposition at the expense of lean deposition. These diets were used to create fat sows at farrowing that had a similar net weight gain during gestation compared with lean sows at farrowing, which received a more optimal diet during gestation.

Body protein reserves

Another reason for fat sows to have a lower voluntary feed intake might be the lower supply of endogenous substrates for milk production (Williams, 1998), which could also be linked to the reduced milk output of fat sows in the studies of Head et al. (1991), and Head and Williams (1991, 1995). Fat sows have less protein reserves to supply substrates for milk production compared with lean animals at a similar weight (Revell et al., 1998a). In studies that changed feeding level during gestation and not diet composition, fat sows were heavier at farrowing (Weldon et al., 1994a, b; Xue et al., 1997; Le Cozler et al., 1998a,b) and may have had a similar or even higher amount of body protein reserves than lean sows. If milk output is limited by the supply of endogenous amino acids, then the capacity of the animal to produce milk is reduced. Limited body protein reserves may therefore reduce milk production and hence the voluntary feed intake of sows (Williams, 1998).

Mahan and Mangan (1975) found that voluntary feed intake during lactation was reduced when sows were fed a diet low in protein during gestation and lactation. However, voluntary feed intake during lactation was not reduced when the diet during gestation was high in protein, indicating that endogenous protein reserves may limit voluntary feed intake under certain circumstances. Mahan (1998) found that multiparous sows consumed more feed during the first week of lactation and primiparous sows during the whole lactation when offered a diet with a higher protein content during gestation. Revell et al. (1998a) used a low and high protein diet during lactation. The dietary supply of protein increased voluntary feed intake during weeks 3 and 4 of lactation, possibly by increasing milk production and hence the drive to consume feed.

In summary, low body protein reserves may limit milk production and, therefore, voluntary feed intake of sows during lactation. However, protein reserves only seem a limiting factor for feed intake when the protein supply of the lactation diet is not optimal in relation to the body composition of the sow.

Meal eating behavior

Dourmad (1993) and Weldon et al. (1994a) studied meal eating behavior during lactation of sows that were fed (close to) ad libitum or restricted during gestation, respectively. Weldon et al. (1994a) found that ad libitum fed, and thus fatter sows, had a lower daily feed intake during lactation by eating fewer meals rather than smaller meals. In contrast, Dourmad (1993) found that fat sows had smaller meals, which were shorter in duration rather than fewer meals, especially during the first two weeks of lactation. Both used a meal criterion of < 10 min to summarize information of feeding bouts into meals. Results of Weldon et al. (1994a) suggest that gastro-intestinal signals mainly affect meal ending, whereas results of Dourmad (1993) suggest that a metabolic control was also partly involved. Both studies agree that fat sows use more time to absorb and utilize ingested nutrients before starting the next meal. This is reflected by the larger meal to meal interval in case of a similar meal size (Weldon et al., 1994a) and a similar meal to meal interval in case of smaller meals (Dourmad, 1993). These results may point towards a higher level of insulin resistance and glucose intolerance of fat sows compared with lean sows.

Effect of body fatness at farrowing on voluntary lactation feed intake in relation to stage of lactation

Revell et al. (1998a) concluded that, during the first two weeks of lactation, voluntary feed intake mainly depends on body fatness whereas, during the latter phase of lactation, also other effects like protein content of the diet may effect voluntary feed intake. Dourmad (1991) and Le Cozler (1999) found that voluntary feed intake during the first part of lactation was significantly affected by body fatness at farrowing, whereas overall lactation feed intake was not. Dourmad (1991) presented regression coefficients of average daily feed intake during different periods of the lactation on backfat thickness at farrowing, which illustrated the same effect. The estimated slope was -63 g d^{-1} mm^{-1} for average feed intake during the whole lactation, whereas the slope was -95 g d^{-1} mm^{-1} when only the average feed intake during week 1 of lactation was considered.

These results are not surprising as differences in fatness between fat and lean sows get smaller during the course of lactation due to the greater losses of tissue of fat sows during the early phase of lactation (Le Cozler et al., 1999).

Optimum body composition at farrowing

It is clear that the sow's feed intake during lactation is controlled in some way and that the ingested nutrients are integrated with body reserves. The amount of body reserves at farrowing has an important influence on subsequent reproductive performance because it determines the extent that reserves can be mobilized during lactation without affecting the interval between weaning and subsequent mating (Mullan and Williams, 1989). High body reserves at farrowing lead to a reduced voluntary feed intake during lactation, as shown above, and excessive weight loss. Excessive weight loss has been associated with several common reproductive problems as already mentioned in the introduction. Also, overfeeding during gestation is not recommended because of the increased frequency of farrowing problems in fat sows (Dourmad et al., 1994). Low feed allowances during gestation lead to an increased voluntary feed intake and consequently less weight loss of sows during lactation. The increase in voluntary feed intake during lactation, however, generally does not compensate for the lower intake during gestation. Therefore, feed intake over the whole cycle of gestation and lactation is reduced when a normal lactation length of about four weeks is considered (e.g., Dourmad, 1991; Xue et al., 1997; Revell et al., 1998a). As a result, a low gestation feeding level decreases backfat thickness and body weight at weaning and tends to delay the return to estrous after weaning, especially in high producing sows (Dourmad, 1991).

Long-term performance of sows is best served by minimizing fluctuations in body weight and fat reserves, so avoiding extremes of body condition and subsequent poor performance (Cole, 1982; Aherne and Kirkwood, 1985). Chemical body composition at farrowing should therefore be considered as an optimum trait, taking the expected reproductive performance and feed intake during the following lactation of sows into account (Dourmad, 1991). For example, Yang et al. (1989) advised a target backfat thickness (P2) at first parturition of 20 mm.

Litter size

In response to greater suckling intensity, sows nursing more piglets produce more milk (Auldist and King, 1995; Toner et al., 1996; Auldist et al., 1998; Revell et al., 1998b). Auldist et al. (1998) estimated a significant linear relationship between milk yield (Y; kg / d) and litter size (LS: 8, 10, 12 or 14 piglets): Y = 5.98 + .689 x LS and Y = 8.20 + .324 x LS for early (day 10 to 14) and late (day 24 to 28) lactation, respectively. Toner et al. (1996) studied milk yield of sows nursing 6, 7, 8 or 10 piglets and also estimated a significant linear relationship between milk yield and litter size. Sows with a greater litter size and milk production have a greater need to use energy and may, therefore, have a larger voluntary feed intake (Figure 1).

Figure 3 shows relationships between lactation feed intake and litter size. Litter size at weaning ranged from 3 to 15 piglets in a data set containing information of 19,393 litters (Koketsu et al., 1996a). As litter size increased from 3 to 13 piglets, average daily feed intake of sows during lactation increased gradually by .6 kg, from 4.4 to 5.0 kg. Weaned litter sizes of 14 and 15 piglets were not associated with a higher lactational feed intake relative to litters having 7 to 13 piglets. O'Grady et al. (1985) estimated in a multiple regression analysis a linear (.22) and a quadratic response [-.01 kg $(pig^2)^{-1}$ d^{-1}] for litter size, indicating a maximum feed intake at a litter size of 14 piglets. According to formulae of O'Grady et al. (1985), daily feed intake increases by .96 kg when litter size increases from 3 to 13 piglets. The intercept A in the study of O'Grady et al. (1985) was arbitrarily taken as 5.2 to avoid an overlap of data points of this study with other studies in Figures 3 and 4. Auldist et al. (1998) studied feed intake of sows nursing 6, 8, 10, 12 or 14 piglets and did not find a linear relationship between feed intake and litter size. However, feed intake of sows nursing six piglets was lowest and feed intake of sows nursing eight piglets was also lower than feed intake of sows nursing larger litters. It should be noted that Auldist et al. (1998) limited daily feed intake to maximally 5 kg.

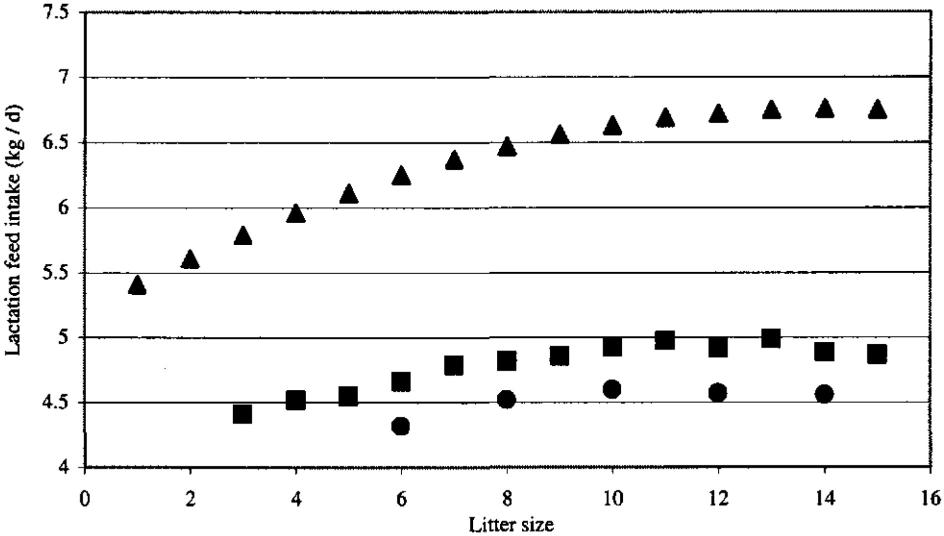

Figure 3. Comparison of the relationships between lactation feed intake and litter size: ■ Koketsu et al. (1996a); ● Auldist et al. (1998); ▲ O'Grady et al. (1985): lactation feed intake = A + .224 x LS – .008 x LS^2 where A corresponds to the intercept and effects of other factors (A arbitrarily taken as 5.2) and LS stands for litter size.

Yang et al. (1989) used different gestation feeding levels over four parities, resulting in lean and fat sows at farrowing. They studied ad libitum feed intake (maximally 7 kg / day) of sows nursing six or ten piglets but did not find a significant effect of litter size on voluntary feed intake. This was especially clear in the lean sows. Fat sows at farrowing nursing 10 piglets, however, had a higher feed intake than fat sows nursing 6 piglets at parities 1 to 4. This indicates that body condition at farrowing might affect a sow's response in feed intake to increasing litter sizes.

In summary, voluntary feed intake of lactating sows nursing relatively small litters increases with increasing litter size. Apparently, factors that limit feed intake of sows nursing small litters can be overridden or terminated when litter size and therefore milk production is increased. The increase in feed intake, however, seems to be following a diminishing increment-type pattern, indicating that limiting factors can only be overridden to a certain extent and / or other factors become limiting for sows nursing larger litters.

Auldist et al. (1998) studied the effect of litter size on a sow's losses of body weight and backfat thickness during lactation and estimated significant positive linear relationships. The increase in voluntary feed intake of sows nursing 6 to 14 piglets was for any increase in litter size inadequate to compensate completely for the increased energy demand. Dourmad (1991), using equations proposed by Noblet and Etienne (1989), calculated that an increase in milk energy output of 1 MJ / d induces a 45 g / day increase in feed intake, which represents only about 40% of supplemental energy required for milk production. Koketsu et al. (1996a) used a general rule of thumb '1.8 kg / d plus .45 kg.piglet^{-1}.d^{-1}', which has been recommended by Tokach and Dial (1992; cited by Koketsu et al., 1996a) as a guideline for producers to use in feeding lactating sows. Sows nursing small litters (< 7 piglets) consumed more than suggested by the guideline, but most sows consumed decidedly less. This illustrates that high producing sows consume an insufficient amount of feed to meet the energy needed to adequately support lactation (Koketsu et al., 1996a).

Parity

Body weight increases with parity. Higher parity (heavier) sows, therefore, have higher maintenance requirements during lactation and may be expected to consume more feed (Figure 1). On the other hand, lower parity sows are still not fully grown and have larger energy and protein requirements for body growth than higher parity sows. Parity number may, therefore, affect the partitioning of energy and / or protein between maternal tissue and milk during lactation. This is supported by Pluske et al. (1998) who made primiparous sows anabolic during lactation by super-alimentation (provide sows with nutrition via stomach cannulae to achieve a feed intake of about 125% of ad libitum). They concluded that primiparous sows seem to partition extra energy into body growth rather than milk production, whereas multiparous sows show an increase in milk yield (Matzat et al., 1990; cited by Pluske et al. 1998)).

Results presented by Cole (1990) suggest that primiparous sows need a higher dietary energy intake to avoid maternal losses in live weight and condition during lactation than second parity sows. This would indicate that primiparous sows have higher maintenance requirements. In particular, primiparous sows are of relatively low absolute size in relation to their productivity and nutrient demands (Whittemore, 1996), which may cause gastro-intestinal limitations to be more severe for primiparous than for higher parity sows. For example, Sinclair et al. (1996) recorded feed intake of primiparous and parity three sows. Sows of both parities had a similar feed intake during the first two weeks of lactation; however, primiparous sows had a lower feed intake during weeks three to five.

Differences in milk yield have been found between parities. However, experiments in which clear conclusions are drawn are scarce, since estimates must be made during successive cycles. Summarizing the results presented by Etienne et al. (1998), milk production increases from the first to second parity, reaches a maximum and is similar from the second to fourth lactation and slowly decreases afterwards. Differences in milk

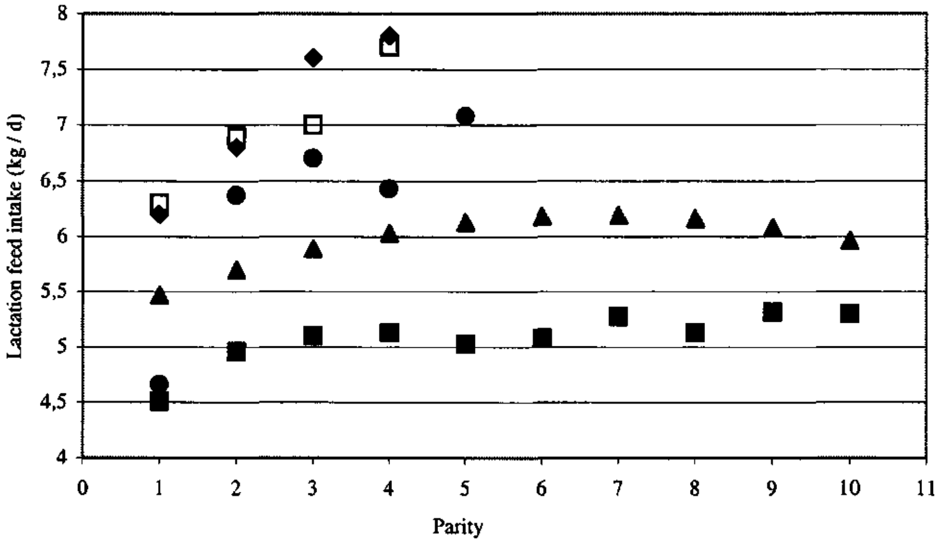

Figure 4. Comparison of the relationships between lactation feed intake and parity: ■ Koketsu et al. (1996a); ● Mahan (1998); ▲ O'Grady et al. (1985); ◆, □ Neil et al. (1996). Within the study of O'Grady et al. (1985): lactation feed intake = A + .297 x P – .022 x P^2 where A corresponds to the intercept and effects of other factors (A arbitrarily taken as 5.2) and P stands for parity. Within the study of Neil et al. (1996): ◆, sows received a simplified diet during the gestation period; □, sows received a conventional diet during the gestation period.

production between parities, however, also partly reflect differences in litter size. According to Ferreira et al. (1988) and Vanschoubroek and Van Spaendonck (1966; cited by Etienne et al. (1998)), second parity sows produced about 11% and 26% more milk, respectively, than primiparous sows.

NRC (1987) summarized voluntary feed intake records from many sources and reported an average daily feed intake during lactation of 5.17 kg per day per sow, with gilts consuming 15% less. Figure 4 shows the relationships between lactation feed intake and parity in four studies. Again, the intercept A in the study of O'Grady et al. (1985) was taken as 5.2, to avoid overlap of data points of this study with the others. O'Grady et al. (1985) estimated in a multiple regression analysis a linear (.30 kg parity number^{-1} d^{-1}) and a quadratic response [-.02 kg $(\text{parity number}^2)^{-1}$ d^{-1}] for parity, with a maximum feed intake between parity 6 and 7. According to this formula, daily feed intake of sows increases by .73 kg from parity 1 to 7. Koketsu et al. (1996a) found a significant lower feed intake for primiparous sows than for older sows in their study about factors affecting lactation feed intake on commercial herds. Feed intake increased by .81 kg, from 4.51 kg (parity 1) to 5.32 kg (parity 9). Mahan (1998) found a significant quadratic increase in weekly and total lactation feed intake by parity (parities 1 to 5); however, litter size during lactation was linearly affected by parity in this study. Mahan (1998) also found an effect of parity that was related to protein content of the diet. A higher protein content in the diet increased voluntary feed intake of primiparous sows during the full lactation, whereas this was not the case for multiparous sows. This may be a reflection of higher maternal protein requirements of primiparous sows; however, lower protein body reserves of primiparous sows may also play a role. Feed intake increased significantly with increasing parity in the study of Neil et al. (1996). They did not present information about levels of litter size; however, they mentioned that litter size increased with parity and that ad libitum feed intake of sows was not affected by litter size.

O'Grady et al. (1985) and Koketsu et al. (1996a) concluded that the gradual increase in feed intake that occurs with advancing parity seems to be consistent with the increase in maintenance energy requirements associated with age-related increases in body weight. Three studies also had body weight and backfat thickness recordings of sows. Primiparous sows lost significantly (Mahan, 1998) or numerically (Sinclair et al., 1996; Neil et al., 1996) more body weight and numerically more backfat thickness (Sinclair et al., 1996; Neil et al., 1996) during lactation compared with multiparous sows. The latter results would indicate that the energy intake increases more than energy requirements for maintenance and milk production of sows with increasing parity. Differences in glucose tolerance between lower and higher parity sows, however, may also play a role. Kemp et al. (1996) orally administrated glucose after an overnight fast at day 105 of gestation to sows of different parities. This resulted in significant higher blood peak levels and area under the curve (up to 75 minutes after administration) of glucose for lower parity sows compared with higher parity sows, indicating that lower parity sows may be more glucose intolerant or insulin resistant.

Genotype

Selection

In several species, feed intake data of lactating animals were recorded to estimate genetic parameters for voluntary feed intake. In a small data set, Van Erp et al. (1998) estimated a heritability of .19 for voluntary feed intake of lactating sows. In dairy cattle, Van Arendonk et al. (1991) estimated a heritability of .46 for dry matter intake, and Koenen and Veerkamp (1998) and Van Elzakker and Van Arendonk (1993) estimated heritabilities varying from .18 to .37 and .18 to .42, respectively, depending on the stage of lactation. These results show that voluntary feed intake of lactating animals is a heritable trait which can be changed by selection.

Kerr and Cameron (1996b) reported substantial variation in feed intake during lactation between primiparous sows of Large White lines after seven generations of divergent selection for lean growth rate, lean feed conversion or daily feed intake during the growth phase from 30 – 85 kg of body weight under ad libitum feed intake (Cameron and Curran, 1994). Lactation feed intake was lowest for sows of the low lean growth rate line and highest for sows of the high daily feed intake and the low lean feed conversion line. Sows selected for low daily feed intake during the growth phase consumed significantly less feed during lactation than sows selected for high daily feed intake (Kerr and Cameron, 1996b). Body weight prior to farrowing and litter size during lactation were not different, whereas backfat thickness prior to farrowing was lower for the low daily feed intake line. The lower feed intake during lactation of sows selected for low daily feed intake, despite a leaner body composition, seems to be contradictory to the previous conclusion that, within genotype, lean sows have a higher feed intake. An explanation for this apparent paradox could be that feed intake during lactation is depending on the difference between the actual body fatness of a sow at farrowing, which mainly depends on the feeding strategy during gestation, and the potential body fatness at farrowing, which depends on the genotype. The smaller the difference between actual and potential body fatness, the lower the feed intake of a sow during lactation would be. This would mean that the sows selected for a low daily feed intake were indeed absolutely leaner, but, compared to their genetic potential for body fatness, relatively fatter than the sows selected for a high daily feed intake. The results of Kerr and Cameron (1996b) are in agreement with the estimated genetic correlation between voluntary daily feed intake during the growth phase and during lactation for pigs (r_g = .92 ± .50; Van Erp et al., 1998). Archer et al. (1998) estimated a genetic correlation of .51 between post weaning voluntary feed intake and feed intake at maturity in mice.

Kerr and Cameron (1996a) estimated genetic relationships between performance traits, measured during the growth phase from 30 – 85 kg of body weight, and reproduction traits. Genetic correlations of average daily feed intake and daily gain during the growth phase with litter weight at weaning were .42 and .52, respectively. This suggests that gilts selected for a high daily feed intake or daily gain during the growth phase exhibit an increase in milk production during lactation, which may affect the voluntary feed intake of these gilts during lactation. Kerr and Cameron (1995, 1996b) reported a reduced daily gain (as a correlated response) of piglets suckling primiparous sows selected for low daily feed intake during the growth phase after five and seven generations of selection. Piglets suckling primiparous sows selected for high daily feed intake did not grow any faster than piglets of unselected control sows (Kerr and Cameron, 1995) or grew only faster during the second part of lactation (Kerr and Cameron, 1996b). These results suggest that a low feed intake of sows can inhibit milk yield rather than that a high feed intake can enhance milk yield (Mackenzie and Revell, 1998).

In conclusion, voluntary feed intake of sows during lactation can directly be changed by selection. In practice, feed intake during lactation may indirectly be changed by selection for production traits, which may also affect litter performance.

Background of genetic differences in lactation feed intake

In general, genetic differences in lactation feed intake of sows will, to some extent, reflect differences in body weight and composition at farrowing, and in litter size and milk production during lactation. Meishan synthetic sows consumed significantly more feed than Large White and Landrace sows (Sinclair et al., 1998). In that study, Meishan sows were significantly lighter, had more backfat at day 1 of lactation and had a larger litter during lactation. Grandhi (1997) did two experiments with Hamshire and Yorkshire sows. During one experiment, Hamshire sows ate significantly more and, in the second experiment, Hamshire sows tended to eat more. These breed differences could at least partly be due to the higher body weight of the Hamshire sows (Grandhi, 1997). Landrace sows produced milk significantly higher in protein content than Duroc sows, whereas fat content was not different (Shurson and Irvin, 1992), which may have contributed to the higher lactation feed intake of Landrace sows in their study.

Differences in glucose tolerance and insulin resistance between lines of sows may also affect voluntary feed intake. Sows of a dam line had significantly higher peak levels of glucose and a higher area under the curve after oral administration of glucose in late gestation compared with sows of a sire line (Kemp et al., 1996). This may point towards a higher level of glucose intolerance and / or insulin resistance of the dam line sows. Breed may also affect the partitioning of nutrients between maternal growth and lactation (Sinclair et al., 1996, 1998) and some breeds may be able to withstand heat stress more effectively than others (Forbes, 1995).

Feed intake regulatory mechanisms that affect voluntary feed intake during early life may, at least partly, also affect voluntary feed intake of mature animals. A number of studies presented results of blood parameters of growing pigs selected for high or low daily gain during the growth phase. In general, pigs of the high gain lines have a higher daily feed intake than pigs of the low gain or control lines. Clutter et al. (1998) found that the high weight gain line had a significantly lower concentration of the putative satiety hormone cholecystokinin per unit of feed consumed compared with the low line. This supports the hypothesis that cholecystokinin may play a role in genetic differences between lines for feed intake. Norton et al. (1989) reported higher blood glucose and insulin concentrations for a high weight gain line whereas blood growth hormone and NEFA concentrations were higher for a low line. In contrast, Arbona et al. (1988) showed greater basal blood growth hormone concentrations for pigs selected for high weight gain than for control pigs. Clutter et al. (1995) reported greater concentrations of circulating IGF-I for high weight gain line pigs compared with low line pigs throughout periods of feed deprivation and refeeding. Altogether, these results indicate that selection for post weaning weight gain resulted in concomitant changes in endocrine and metabolic status of growing pigs.

It is generally assumed that feed intake regulatory mechanisms are similar for mammalian species and chickens, although there are also some differences (Barbato, 1994). Chickens selected for a high gain voluntarily consumed a volume of feed approaching the full capacity of their gastrointestinal tract, whereas chickens selected for a low daily gain consumed a small percentage of total capacity (Barbato et al., 1984). Selection for body weight gain increased villus surface area by 20-fold due to increases in crypt size and enterocyte migration rates (Smith et al., 1990; cited by Barbato, 1994). The latter results, however, could also be due to the positive relationship between feed intake and villus surface area (Goodlad et al., 1987; cited by Barbato, 1994). O'Sullivan et al. (1992) found that high gain line chickens had significantly higher levels of the enzyme trypsin than low gain line chickens of similar body weight or age. Furthermore, data reported by Barbato (1994) suggest a genetic basis for CNS neurotransmitter levels, which seems to be related to selection for weight gain.

In summary, results presented above show that differences between breeds or lines of breeds in voluntary feed intake of lactating sows may involve a large number of factors in addition to body weight and body condition of sows and litter size (milk production) during lactation. Though there is a dearth of information regarding the genetics of central and peripheral feed intake control mechanisms, it seems that mechanisms may act at the pre- and post-absorptive level, which shows that each factor mentioned in Figure 1 could be involved. An increase in voluntary feed intake by selection is likely accomplished by canceling or reducing effects of the most limiting factor(s), whereas a decrease is likely accomplished by introducing new or intensifying effects of existing limiting factor(s).

Conclusions and implications

This review showed that the sow factors body composition at farrowing, litter size during lactation, parity and genotype affect the voluntary feed intake of lactating sows. As mentioned in the introduction, fatness at farrowing of young sows tends to decrease due to selection, while the number of piglets to be weaned per sow per litter and milk production of lactating sow tend to increase. These trends result in higher energy requirements of the sow during lactation, but body fat reserves to support these extra requirements are reduced. As illustrated, lactating sows compensate for the larger energy requirements due to increasing litter size (milk production) during lactation by increasing their feed intake. The compensation, however, is not complete for small and medium litters and seems to be absent for large litters. These effects are illustrated by larger weight and backfat losses of sows with increasing litter size.

Continued selection for increasing energy requirements during lactation will result in an increasing number of sows that consume an insufficient amount of feed to adequately support lactation. In addition, continued selection for production traits may further reduce body fatness of young sows. This will probably increase early culling of young sows due to reproductive failures and reduce lifetime performance of sows. For a sustainable production, the trends of increasing energy requirements and decreasing body fat reserves should be accompanied by a higher feed intake of sows during lactation. This may be realized by changing sow, environmental and / or dietary factors. In practice, body composition at farrowing and genotype are the two sow factors that best can be used to increase feed intake capacity during lactation. Of these, genotype seems the most appropriate as body composition at farrowing should be considered as an optimum trait and, from this point of view, voluntary feed intake during lactation should not be maximized per se, for example, by reducing feeding level during gestation. These results, therefore, suggest that voluntary feed intake during lactation should be included in breeding programs. A higher feed intake during lactation may be accomplished by direct selection for lactation feed intake or indirect selection, for example, for daily gain or daily feed intake during the growth phase.

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7 The Importance of a High Feed Intake during Lactation of Primiparous Sows Nursing Large Litters

The objective of this study was to investigate whether nursing a large number of piglets has negative effects on lactation and post-weaning performance of primiparous sows and if a greater lactation feed intake can prevent possible negative effects. Data were recorded on 307 ad libitum fed sows of three genotypes in an experiment where litter size was standardized to 8, 11 or 14 piglets during a four-week lactation. Daily feed intake of sows was not affected by litter size for two genotypes, whereas it was curvelinearly affected for the third genotype ($P < .05$) with a maximum at 10.8 piglets. Backfat loss of the sows increased linearly with litter size ($P < .05$) for two genotypes. In the third genotype backfat loss increased only at litter sizes > 9.8 piglets ($P < .01$). Body-weight loss of the sow and litter weight gain increased linearly with litter size ($P < .001$). Differences in responses to increasing litter size found between the three genotypes may be related to differences in feed intake pattern during lactation, upper critical temperature, and body composition of sows. Sows nursing more piglets during lactation had a higher probability of a prolonged weaning-to-estrus interval (odds ratio of litter size was 1.23; $P < .10$). A higher daily feed intake during lactation reduced tissue loss of the sow and increased litter weight gain ($P < .01$), and reduced the probability of a prolonged weaning-to-estrus interval (odds ratio of feed intake was .58; $P < .01$). At high levels of litter size, a one-kg increase in feed intake resulted in a lower output, measured as reduced body tissue loss or increased litter weight gain, compared with low levels of litter size. This may be related to higher maintenance requirements of sows due to heat stress and (or) less optimal conditions for piglet weight gain at high levels of litter size. Selection for a larger feed intake during lactation and improvement of environment and diet factors to reduce occurrence of heat stress is recommended.

Keywords: Feed intake, Backfat loss, Weight loss, Litter size, Reproductive performance, Sows

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Eissen, J.J., E.J. Apeldoorn, E. Kanis, M.W.A. Verstegen, and K.H. de Greef. The importance of a high feed intake during lactation of primiparous sows nursing large litters.

Introduction

Genetic and environmental changes during the last decades have increased litter size and milk production of sows (Southwood and Kennedy, 1991; Knap et al., 1993; Mackenzie and Revell, 1998). For example, Knap et al. (1993) estimated a realised yearly selection response of around .045 piglets per litter for first-parity sows. Because the nutritional and energy requirements of lactating sows are closely related to milk production (Noblet et al., 1990) nutritional and energy requirements of sows during lactation have increased as well. At the same time, the amount of body fat reserves of young sows to support extra requirements has decreased (Whittemore, 1996). Besides, voluntary feed intake of lactating sows has not increased in proportion with the higher energy requirements (Noblet et al., 1998), or may even has decreased (Kerr and Cameron, 1996).

Nursing a larger litter increases losses of backfat thickness and body weight of sows during lactation (Yang et al., 1989; Auldist et al., 1998). Excessive loss of body tissue during lactation has been shown to prolong weaning-to-estrus interval, to decrease ovulation and conception rate, and to increase incidence of anestrus and embryonic mortality in experiments where feed intake was restricted during lactation (e.g. Reese et al., 1982; Kirkwood et al., 1987; Prunier et al, 1993; Zak et al., 1997). Nowadays, inadequate feed intake during lactation is particularly evident in primiparous sows because, relative to multiparous sows, they have less body reserves and a lower daily feed intake. Moreover, primiparous sows need extra energy for body weight gain as they are physiologically younger (NRC, 1987).

Shurson and Irvin (1992), Adamec and Johnson (1997), and Ten Napel et al. (1998) showed that selection for reduced body fatness of sows, higher litter size and (or) higher milk production may negatively affect post-weaning reproductive performance of sows. Continued selection for leanness and reproduction, without increasing lactation feed intake, will likely result in a larger proportion of, especially, young sows consuming an insufficient amount of feed to adequately support lactation. This will probably result in more culling due to reproductive failures and a reduced lifetime performance of sows (Eissen et al., 1999). An experiment was set up to simulate possible future high levels of litter size on current lactating primiparous sows. It was studied whether nursing a large litter has negative effects on sow performance during lactation and post weaning. Ad libitum feed intake during lactation of each sow was recorded to study if a larger feed intake can prevent possible negative effects of large litters on sow performance, and if selection for lactation feed intake should be recommended.

Materials and methods

Experimental Design

Data were recorded on 307 primiparous sows of a commercial purebred Landrace sow line breed (genotype 1, n = 117) and two commercial Landrace / Yorkshire based crossbred sow lines (genotype 2 (n = 55) and genotype 3 (n = 135)), which were F1 progeny of genotype 1 sows and two different sow line breeds, respectively. Data were recorded in the experimental farm of IPG in Beilen, from October 1996 till October 1998. Before farrowing, gilts were randomly assigned to a target litter size of 8, 11 or 14 piglets during lactation. Assignment was within genotype and, if possible, within full sib family. Litter size was standardized to the target number by crossfostering within three days after farrowing. Only piglets > 1 kg of body weight were used for crossfostering. Litter size was standardized to a lower number if the number of piglets available for crossfostering was inadequate. All sows were fed ad libitum during lactation. Creep feed was not available for the piglets throughout lactation.

Management

Gilts conceived pregnancy at an average age of 232 d (SD 17) with a minimum and maximum age of 200 and 303 days, respectively. Each gilt was allowed to return to estrus once after first insemination. Gilts were housed in individual pens during gestation. At d 105 (SD 4.14) of gestation, gilts were moved to a standard farrowing crate until weaning at about d 28 of lactation, at which time they were transferred again to the individual pens.

During gestation, three diets were used in the course of the experiment, containing 12.58 to 12.84 MJ DE and 140 to 162 g CP per kg, respectively. Sows were fed according to a commercial Dutch feeding regime to attain a target of 16-20 mm backfat thickness at farrowing. The amount of feed daily offered gradually increased from about 1.8 kg at insemination to 3.2 kg during late gestation. Depending on a subjective scoring of fatness, individual sows received extra feed per day varying from 0 to 20%. During lactation, also three diets were used in the course of the experiment containing 13.34 to 14.09 MJ DE and 163 to 180 g CP per kg, respectively. Feed intake per sow was linearly transformed to feed intake of a diet containing 13.72 MJ DE per kg, which was the energy content of the intermediate diet. The level of feeding was progressively increased from parturition onwards to reach ad libitum from about d 4 post-farrowing. Feed was given at 0700 and 1500, in approximately equal amounts, with more or less added to the feeders to ensure that feed was always available and fresh. The water nipple was above the trough and water was available ad libitum to the sows.

Minimum room temperature in the farrowing crates was maintained between 17 and 21 °C, depending on stage of lactation. Maximum room temperature depended on the outside temperature. Farrowing crates had floor heating for piglets. During the first three days after farrowing, supplemental heat was also provided by an infra red heater in winter. Artificial lighting was present from 0700 till 1530. The amount of natural lighting was limited. Routine management procedures were followed in caring for the sow and litter during parturition and lactation.

Piglets were weaned at about 28 d of lactation. From three or four days after weaning onwards, sows were tested each morning for the onset of standing estrus using direct exposure to a boar. Sows were also checked for other signs of estrus such as vulval swelling and reddening and reaction to back-pressure. After weaning, sows were fed the lactation diet (close to) ad libitum until reaching first estrus. When sows did not show estrus within the first week, daily feed allowance was set to maximally 2.5 kg.

Traits

It was assumed that sows have reached their maximum feed intake capacity by d 10 of lactation (Revell et al., 1998). Total ad libitum feed intake of the sow was recorded from d 10 (mean 10.4; SD 1.8) of lactation until weaning at d 28 (mean 27.8; SD 1.9). Sows and litters were weighted when feed intake recording started and ended. Then also the depth of backfat of sows was measured by ultrasound at three positions along the back at both sides. Piglets that died between d 10 of lactation and weaning were recorded and weighed. Weaning-to-estrus interval was defined as the interval from weaning to standing estrus.

Total feed intake was adjusted linearly to total feed intake from d 10 till d 28 of lactation (weaning) using a within genotype regression of feed intake on day numbers of lactation. Average daily feed intake was calculated as the total feed intake from d 10 till d 28 divided by 18. Sow and litter weights and average backfat thickness of sows not measured exactly at d 10 or d 28 of lactation were adjusted linearly to d 10 and 28, respectively, using a within genotype regression. The daily loss of backfat thickness and body weight of sows during lactation was defined as the average daily decrease from d 10 till d 28, respectively. The body weight of piglets that died between d 10 and d 28 was added to the litter weight of the sow at d 28. Litter weight gain was defined as the average daily increase in litter weight from d 10 till d 28. Piglet weight gain was defined as litter weight gain divided by litter size during lactation. Litter size during lactation (from d 10 till d 28) of a sow was corrected for piglets that died between d 10 and weaning. Each dead piglet was counted as (day number of lactation of dying - 10) / (28 – 10) piglet. For example, litter size during lactation was 12.33 when litter sizes at d 10 and weaning were 13 and 12, respectively, and one piglet died at d 16 of lactation.

Statistical Analysis

Analysis was performed in two steps. In the first step, effects of litter size and genotype on lactation feed intake and sow performance were studied. In the second step, the partitioning of consumed feed over maternal and litter use was studied. Data of nine sows were not included in the analyses due to illness of the sow or litter. Data of seven sows were not included in the analyses because litter size at weaning was < 7 piglets and the focus of the study was on large levels of litter size. Litter size was used as a continuous and not as a class variable in the analyses because a substantial number of sows had a litter size unequal to 8, 11 or 14 piglets at d 10 of lactation and (or) at weaning (Table 1). This was due to incomplete standardization after farrowing and piglet mortality. Furthermore, treating litter size as a continuous variable enabled correction of litter size during lactation for piglet mortality, as illustrated above, and provided estimates of relationships between litter size and sow performance.

Table 1. Distribution of sows over litter sizes at d 3 and d 10 of lactation and at weaning

	Litter size							
Time	7	8	9	10	11	12	13	14
Day 3 of lactation[a]	7	87	2	17	90	8	16	62
Day 10 of lactation	13	81	9	26	79	9	25	49
Weaning	29	70	8	38	68	16	25	37

[a] Data of two sows have not been included in this row because their litter size was standardized after d 3 of lactation

For step 1, each trait measured during lactation was analyzed using the GLM Procedure of SAS (SAS, 1990). The initial model included the following traits:

$$Y = \beta_0 + G + \beta_1\, LS + \beta_2\, LS^2 + \beta_3\, LS{:}G + \beta_4\, LS^2{:}G + \beta_5\, AF + \beta_6\, AF{:}G + YS + Error$$

Where Y = dependent variable, G = genotype of the sow; LS = litter size during lactation; AF = age at farrowing; YS = year-season of farrowing (clusters of three months; 9 classes). Genotype, the linear effect of litter size, and year-season were included in the model independent of significance for each trait. Backward elimination was used for modeling of other terms ($P < .10$).

Table 2. Least-squares means per genotype and regression coefficients of sow performance traits (measured from d 10 till d28 of lactation) on litter size

Item	Lsmeans genotype (G)[a]			Litter size[b, c]		RSD[d]
	G1	G2	G3	L	Q	
Sow lactation feed intake (kg / d)	4.64[x]	4.82[xy]	5.03[y]	[.40[NS]][e]	[-.018[NS]][e]	.92
Sow backfat (mm)						
At weaning	13.97[x]	14.03[x]	11.88[y]	-.31[***]	NS	2.10
Loss during lactation (mm / d)	.137	.152	.144	[-.014[NS]][f]	[.0013[NS]][f]	.077
Sow body weight (kg)						
At weaning	148.72[x]	146.19[x]	159.37[y]	4.97[NS]	-.35[†]	13.72
Loss during lactation (kg / d)	.92[x]	1.12[y]	.97[xy]	.086[***]	NS	.51
Litter weight (kg)						
At weaning	75.36[x]	76.74[xy]	79.43[y]	3.78[***]	NS	8.04
Increase during lactation (kg / d)	2.26[x]	2.24[x]	2.39[y]	.071[***]	NS	.35
Piglet weight (kg)						
At weaning	7.42[x]	7.61[xy]	7.78[y]	-1.01[***]	.031[**]	.79
Increase during lactation (kg / d)	.224[x]	.224[x]	.237[y]	-.039[***]	.0011[*]	.034

[a] Genotype abbreviations: G1, genotype 1; G2, genotype 2; G3, genotype 3

[b] Litter size abbreviations: L, linear effect of litter size; Q, quadratic effect of litter size

[c] NS = not significantly different from 0 ($P \geq .10$), † $P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$

[d] RSD = residual standard deviation

[e] The interactions between genotype and the linear and quadratic effects of litter size were significant ($P < .10$; Presented coefficients for litter size are estimates without including these interactions in the model.

[f] The interactions between genotype and the linear and quadratic effects of litter size were significant ($P < .01$; Presented coefficients for litter size are estimates without including these interactions in the model.

[x, y, z] within a row, lsmeans lacking a common superscript letter differ ($P < .05$)

To determine risk factors affecting occurrence of prolonged weaning-to-first-estrus intervals, logistic regression analysis were performed using the LOGISTIC procedure of SAS (SAS, 1996). A weaning-to-estrus interval up to 7 d was considered as normal (Ten Napel et al., 1995), whereas longer intervals were considered as prolonged. Genotype, litter size during lactation, and year-season of farrowing were included in the model independent of significance. Other effects tested were age at farrowing and lactation length ($P < .10$).

For step 2, relationships between average daily feed intake during lactation and body tissue losses of the sow, litter weight gain, weaning-to-first-estrus interval were computed. For step 2, the model of step 1 was extended with the following terms:

$$Y = \text{model step 1} + \beta_7\,\text{ADFI} + \beta_8\,\text{ADFI:G} + \beta_9\,\text{LS} \times \text{ADFI}$$

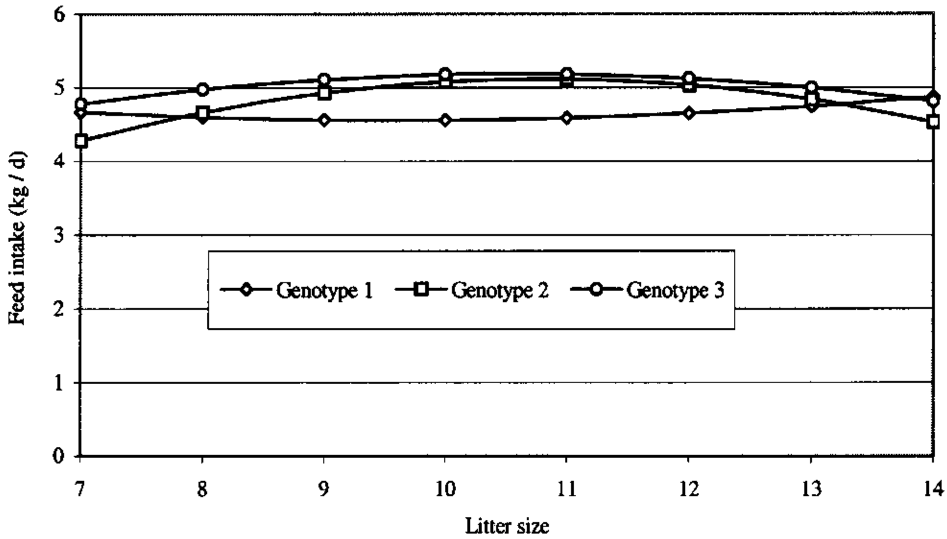

Figure 1. Influence of litter size (LS) on average daily feed intake (FI) of the sow from d 10 till d 28 of lactation. Genotype 1: FI = 6.08 - .32 × LS + .017 × LS^2; Genotype 2: FI = -1.62 + 1.25 × LS - .058 × LS^2; Genotype 3: FI = 1.61 + .68 × LS - .032 × LS^2.

Where Y = loss of backfat thickness or body weight of the sow or litter weight gain during lactation; ADFI = average daily feed intake during lactation. Interactions between average daily feed intake and genotype and litter size were only included when significant ($P < .10$). To study effects of feed intake on prolonged weaning-to-estrus intervals, average daily feed intake during lactation was included in the logistic regression analysis of step 1.

Results

Influence of genotype and litter size on sow performance

Average litter size at d 3 after standardization, at d 10 of lactation and at weaning (Table 1) was 10.75, 10.54, and 10.30, respectively, and was not affected by genotype. Table 2 shows the effects of genotype and litter size on sow performance. Figures 1 to 3 present the effects of litter size on feed intake and body tissue losses of the sow, and litter and piglet weight gain. Results are plotted for the average genotype when interactions between litter size and genotype were not significant ($P \geq .10$). Genotype 3 sows had a higher average daily feed intake than genotype 1 sows. Average daily feed intake was curve-linearly affected by litter size only for genotype 2 sows ($P < .05$; Figure 1), though the course of feed intake was similar for genotype 3 sows. Genotype 2 sows reached a

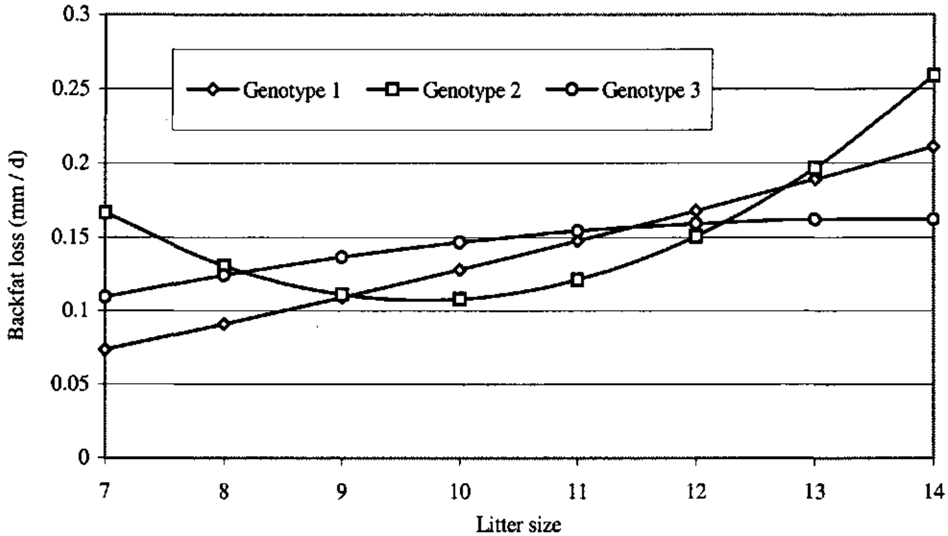

Figure 2. Influence of litter size (LS) on loss of backfat thickness (LBF) of the sow from d 10 till d 28 of lactation. Genotype 1: LBF = -.028 + .012 × LS + .00037 × LS^2; Genotype 2: LBF = .88 - .16 × LS + .0082 × LS^2; Genotype 3: LBF = -.065 + .033 × LS - .0012 × LS^2.

maximum feed intake at 10.8 piglets a litter. Feed intake of genotype 1 and 3 sows was not significantly affected by litter size as regression coefficients were .036 (P = .38) and -.0010 (P = .98) kg / piglet, respectively, when only the linear effect of litter size was included in the model.

Genotype 3 sows were heavier and had less backfat at weaning than sows of both other genotypes. Litter size during lactation reduced backfat thickness and body weight of sows at weaning in a linear and curve-linear way, respectively. Daily backfat loss was curve-linearly affected by litter size only for genotype 2 sows (P < .01; Figure 2): backfat losses decreased when litter size increased up to 9.8 piglets, after which losses increased again. When only the linear effect of litter size was included in the analysis, loss of backfat thickness increased with .020 (P < .001) and .0073 (P < .05) mm / piglet for genotype 1 and 3 sows, respectively. The daily loss of body weight during lactation was higher for genotype 2 than genotype 1 sows and increased linearly with litter size (Figure 3). Litter and piglet weight gains during lactation were significantly larger for genotype 3 sows. Litter weight gain increased linearly with litter size, whereas, piglet weight gain decreased curve-linearly with litter size (Figure 3).

A proportion of 56, 37, and 20% of sows of genotype 1, 2, and 3, respectively, had a prolonged interval from weaning-to-estrus. Logistic regression analysis revealed that genotype and litter size affected the probability of a prolonged interval weaning-to-estrus

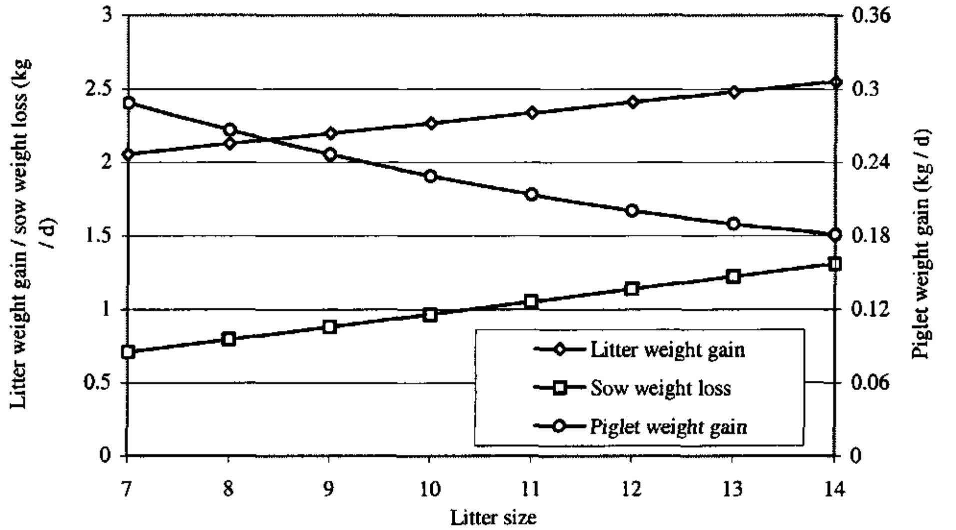

Figure 3. Influence of litter size (*LS*) on loss of body weight (*LBW*) of the sow and on a sow's litter (*LWG*) and piglet (PWG) weight gains from d 10 till d 28 of lactation. Lines are plotted for the average genotype, as the effects of litter size were not affected by genotype ($P \geq .10$). LBW = .11 + .086 × LS; LWG = 1.56 + .071 × LS; PWG = .51 - .039 × LS + .0011 × LS^2.

significantly. The odds ratio, defined as the probability of having a prolonged interval over the probability of not having a prolonged interval, was 1.23 for litter size ($P < .01$). This indicates that a sow is 1.23 times as likely to have a prolonged interval when nursing one extra piglet during lactation. For example, a sow nursing 11 piglets is 1.51 (1.23^2) times as likely to have a prolonged interval as a sow nursing 9 piglets. Furthermore, genotype 1 and 2 sows were 5.47 ($P < .01$) and 2.03 ($P < .10$) times as likely to have a prolonged interval as genotype 3 sow. Genotype 1 sows were 2.70 ($P < .05$) times as likely to have a prolonged interval as genotype 2 sows. When regression was performed per genotype separately, the odds ratio remained significantly > 1 for genotype 1 sows (odds ratio = 1.37 ($P < .01$), whereas, the ratios for genotype 2 and 3 sows were 1.21 and 1.13, respectively, which was not different from 1. The non-significant result for genotype 2 sows was due to the smaller number of genotype 2 sows compared with both other genotypes.

Relationships between daily feed intake and sow performance

An increase in voluntary average daily feed intake reduced backfat and weight losses of sows and increased litter weight gain (Table 3). The favorable effect of feed intake on losses of backfat and body weight was smaller at larger litter sizes. For example, a one kg increase in daily feed intake reduced daily backfat and weight loss with .023 (= -.0911 + (10 × .00685)) mm and .13 (= -.428 + (10 × .0295)) kg, respectively, at a litter size of 10 piglets. At 14 piglets, however, a one kg increase in feed intake reduced weight loss only .015 kg / d, whereas, backfat loss was not reduced at all (coefficient +.0048 mm / d). The regression coefficient of feed intake on litter weight gain was larger for genotype 2 than genotype 1 sows, but was not affected by litter size.

Table 3. Regression coefficients of sow performance traits (measured from d 10 till d 28 of lactation) on average daily feed intake in relation to genotype and litter size

Item	Feed Intake[a]	Feed intake (within genotype)[a, b]			Litter size × Feed intake[a]	RSD[c]
		G1	G2	G3		
Backfat thickness loss (mm / d)	-.091***		NS		.0069**	.075
Body weight loss (kg / d)	-.43**		NS		.030*	.49
Litter weight gain (kg / d)	***	.058†, x	.19***, y	.12**, xy	NS	.34

[a] NS = not significantly different from 0 (P ≥ .10), † P < .10, * P < .05, ** P < .01, *** P < .001

[b] Genotype abbreviations: G1, genotype 1; G2, genotype 2; G3, genotype 3

[c] RSD = residual standard deviation

[x, y, z] within a row, genotype values lacking a common superscript letter differ (P < .05)

A greater feed intake during lactation reduced the probability of a prolonged weaning-to-estrus interval (odds ratio = .58; P < .001). The odds ratios were .44 (P < .01), .63 (P = .14), and .58 (P < .10) for genotype 1, 2, and 3 sows, when analyses were performed per genotype. The non-significant result of genotype 2 sows was due to the smaller number of animals. The odds ratio for feed intake was .45 (P < .01) and .61 (P < .05) for sows with a litter < 11 piglets and ≥ 11 piglets, respectively, when analysis was performed in two sub sets differing in number of piglets per sow. The latter results suggest that a greater feed intake is more favorable for the sow at a lower litter size.

Discussion

Influence of genotype and litter size on sow performance

In general, present results for the effect of litter size on sow performance during lactation are in line with literature (Yang et al., 1989; Auldist et al., 1998): ad libitum daily feed intake of sows was not or only a little affected by litter size and losses of backfat thickness and body weight were higher with increasing litter size. Also the positive effect of litter size on litter weight gain is in agreement with literature (Yang et al., 1989; Koketsu et al., 1996b; Koketsu and Dial, 1997; Auldist et al., 1998). Sows of the three genotypes, however, responded not completely similar to increasing litter size, indicated by significant interactions between genotype and litter size for daily feed intake and backfat loss. Differences in feed intake pattern during lactation, upper critical temperature and body composition between sows of the three genotypes may have contributed to different responses to increasing litter size. Before discussing these items, the non-significant curve-linear effects of litter size on weight loss of the sow and litter weight gain are described per genotype, because these relationships are helpful for parts of the discussion. The pattern of the effect of litter size on weight loss was similar to results for backfat loss. Weight loss increased linearly with litter size for genotype 1 sows, was not affected at litter sizes < 10 piglets but increased at larger litter sizes for genotype 2 sows, and showed a diminishing increment-type pattern with litter size for genotype 3 sows. Litter weight gain increased linearly with litter size for genotype 1 sows, increased linearly with litter size up to 10-11 piglets, after which it started plateauing for genotype 2 sows, and showed a diminishing increment-type pattern with litter size at levels > 11 piglets for genotype 3 sows.

The absence of a significant effect of litter size on daily feed intake for genotypes 1 and 3 sows is in agreement with literature, in which litter size during lactation was six or 10 piglets (Yang et al., 1989) or ranged from six to 14 piglets (Auldist et al., 1998). It should be noted, that daily feed intake was restricted to maximally 7 and 5 kg per sow in the experiments of Yang et al. (1989) and Auldist et al. (1998), respectively. O'Grady et al. (1985) and Koketsu et al. (1996a) found an increase in feed intake with increasing litter size for small and medium litters as in present study for genotype 2 sows. O'Grady et al. (1985) estimated a maximum feed intake at a litter size of 12.8 to 14 piglets and Koketsu et al. (1996a) concluded that feed intake did not significantly increase beyond litter sizes of 11 piglets. The increase in daily feed intake with increasing litter size for small and medium litters was larger in present study compared to both others. For example, daily feed intake increased with .44, .16 and .18 kg when litter size increased from 8 to 11 piglets in the present study, the study of Koketsu et al. (1996a), and the study of O'Grady et al. (1985), respectively. This relatively large increase for genotype 2 sows was matched by the small decrease in backfat loss (Figure 2) and the absence of an effect of litter size on weight loss at litters < 10-11 piglets.

Feed intake decreased significantly (coefficient = -.27 kg / piglet; $P < .10$) and numerically (coefficient = - .13 kg / piglet; $P = .25$) for genotype 2 and 3 sows, respectively, when analyses were performed in a data set containing only information of sows with ≥ 10.8 piglets. Two points that may have contributed to a reduced feed intake from d 10 till weaning at higher levels of litter size are discussed. The first point relates to the pattern of feed intake. Koketsu et al. (1996a) found that greater feed intake during early lactation was associated with greater occurrence of feed intake drops during later lactation. Sows that showed a drop in their feed intake pattern ended up with a significant lower average daily feed intake during lactation compared to sows not showing a drop. Albeit not significant, genotype 2 sows had numerically the highest average daily feed intake during the first 10 days of lactation in present study, followed by genotype 3 sows. Furthermore, average daily feed intake during the first 10 days increased with increasing litter size at litter sizes > 12 piglets for genotype 2 sows. Both aspects may have caused most drops to occur in genotype 2 sows during later lactation, especially in sows nursing large litters, which may have contributed to the lower daily feed intake from d10 till weaning at high levels of litter size. The second point relates to the occurrence of heat stress. An increasing litter weight gain indicates that sows nursing a larger litter have a higher milk production and, therefore, a higher level of metabolic activity and heat production. As a consequence, sows nursing a large litter have a lower upper critical temperature and may be expected to suffer more from heat stress at a certain temperature than sows nursing smaller litters. Lactating sows suffering from heat stress reduce heat production by reducing their feed intake and increasing their tissue mobilization (Black et al., 1993; Messias de Bragança et al., 1998). By using nutrients from body reserves instead of nutrients from the diet, the sow reduces total metabolic heat production by reducing digestion heat production. Genotype 2 and, to a lesser extend, genotype 3 sows may then suffer from heat stress at higher levels of litter size. Genotype 2 sows are increasing body tissue mobilization at higher levels of litter size. They, however, are not able to continue the trend of increasing litter weight gain with increasing litter size at litters > 11 piglets as mentioned earlier. The latter may partly be due to an increase in blood flow to the skin to assist heat loss, at the expense of blood flow, and thus nutrients, to the mammary gland (Black et al., 1993). Genotype 3 sows are not increasing body tissue mobilization at larger levels of litter size to compensate for a decreasing feed intake, which is confirmed by a diminishing increment-type pattern of litter weight gain with litter size at levels > 11 piglets. Genotype 3 sows may not be willing to increase body tissue mobilization due to the lower level of backfat thickness and, therefore, body fat reserves compared to genotype 2 sows or may also have a reduced flow of nutrients to the mammary gland.

The larger feed intake of genotype 3 compared with genotype 1 sows may have caused the larger litter weight gain, as backfat and weight losses during lactation were not different (Table 2). Moreover, for the heavier genotype 3 sows, 1 mm of extra backfat loss means a greater loss of subcutaneous fatness than for both other genotypes. Litter weight gain was not higher for genotype 2 compared with genotype 1 sows, though daily weight loss was significantly higher and daily feed intake and backfat loss were numerically higher for genotype 2 sows. Effects of heat stress may have contributed to this result. Sows suffering from heat stress increase heat loss, particularly from the lungs through higher respiratory rate in order to avoid excessive increase in body temperature (Black et al., 1993; Johnston et al., 1999). However, this active way of losing heat will increase maintenance requirements. The hypothesis that increasing maintenance requirements of genotype 2 sows with increasing litter size due to heat stress may have contributed is supported by the following observation. When only sows with litters ≤ 11 piglets were included in the analyses, differences in least-squares means for feed intake and loss of backfat and body weight between genotype 1 and 2 sows were very similar with results presented in Table 2. However, litter weight gain was higher for genotype 2 sows (2.23 vs 2.15 kg / d).

The larger weight and backfat losses with increasing litter size resulted in a higher probability of a prolonged weaning-to-estrus-interval for genotype 1 and 2 sows. Some studies also indicated an unfavourable association between litter size during lactation and weaning-to-estrus interval (e.g., Sterning et al., 1990; Vesseur et al., 1994; Vesseur et al., 1996), whereas others did not (e.g., Tubbs et al., 1990; Koketsu and Dial, 1997). Breed differences in length of weaning-to-estrus interval are known to exist (Vesseur et al., 1996) and may have contributed to differences in odds ratios for a prolonged interval between the three genotypes.

In total, 191 of the 307 animals were inseminated after weaning on the day(s) of standing estrus and have a record for size of second litter, which were 55, 43, and 93 sows of genotype 1, 2, and 3, respectively. Sows that produced a second litter had more backfat and a higher body weight at weaning, and a larger feed intake during their first lactation ($P < .05$) compared to sows that did not produce a second litter. Furthermore, litter size during first lactation was smaller ($P < .10$) for sows that had a record for size of second litter. Size of the second litter was reduced when litter size during first lactation was > 9.6 piglets ($P < .05$). This is in line with literature as Sterning and Lundeheim (1995) found that the probability of having a large second litter was low for sows with a large first litter. Also Morrow et al. (1992) concluded that a large first litter was the major determinant of less pigs being born alive in the second litter. The actual relation with litter size may have been stronger than observed, as the sows that produced a second litter were on average in better condition than sows that did not produce a second litter, and carry over effects can be expected especially in the leaner sows.

Relationships between daily feed intake and sow performance

A greater lactation feed intake of the sow had favorable associations with sow performance, both during lactation and post weaning. In literature, relationships between daily feed intake and sow performance were mostly studied in experiments in which feed intake was restricted during (part of) lactation. In a number of these experiments, litter weight gain was not affected by feed intake as feed restricted sows simply mobilized more body reserves to compensate for the lower feed intake (e.g. Reese et al., 1982; Prunier et al., 1993; Zak et al., 1997). In other experiments, feed restricted sows showed a lower litter weight gain (e.g., Reese et al., 1982, Eastham et al., 1988; Mullan and Williams, 1989), possibly because the amount of sow body reserves was insufficient or less mobilizable, or the level of feed intake restriction was more severe compared to experiments where litter weight gain was not affected. Koketsu et al. (1997b) found that litter weight gain increased by about .035 kg / d per kg increase in daily feed intake during weeks 2 and 3 of an, on average, 19-day lactation period for ad libitum fed primiparous sows, which is less than in present experiment. Pluske et al. (1998) superalimented primiparous sows and found that extra feed (energy intake of superalimented sows was 38% higher then ad libitum fed sows) was rather partioned in the sow's body than into milk production as litter growth of superalimented and ad libitum fed sows were similar. A greater daily feed intake reduced the weaning-to-service interval in studies of Koketsu and Dial (1997) and Koketsu et al. (1997b). Koketsu et al. (1997a) estimated odds ratios for the effect of lactation feed intake ranging from .82 to .89 for regularly and irregularly returning to service, anestrus, and not farrowing. These results support the finding that a larger feed intake reduces the risk of post weaning reproductive problems.

Genotype 2 sows partitioned more feed to litter weight gain than genotype 1 sows. Although the interaction between genotype and feed intake was not significant ($P = .43$), genotype 2 sows used less feed for backfat loss reduction than genotype 1 sows, with genotype 3 sows being intermediate of both. The effect of genotype on the relationship between feed intake and body weight loss was neglectable ($P = .92$). Odds ratios for the effect of feed intake on weaning-to-estrus interval, being highest for genotype 2 and lowest for genotype 1 sows, were in line with the result found for backfat loss and litter weight gain.

At higher levels of litter size, less feed was used to reduce weight and backfat losses but litter weight gain was not affected ($P = .99$). This indicates that a one-kg increase in feed intake resulted in a lower output, measured as reduced body tissue loss or increased litter weight gain, at higher levels of litter size. The result that sows with < 11 piglets had a lower odds ratio for the effect of feed intake on weaning-to-estrus interval than sows with ≥ 11 piglets is in line with the finding that less feed is partitioned in body growth at higher levels of litter size. Three points that my have contributed to a lower output per kg increase in feed intake at higher levels of litter size can be forwarded. Firstly, an increase in feed intake at higher levels of litter size may again cause heat stress and increase maintenance requirements of sows nursing large litters, resulting in a lower output per kg increase in feed intake. Secondly, sows nursing a large litter are in a situation of severe catabolism, which might affect milk composition and result in a sub-optimal milk composition for litter weight gain (Pluske and Dong, 1998). Thirdly, piglets in a large litter may have higher maintenance requirements associated with increased physical activity due to an increasing number of sucklings as piglets try to increase their milk intake (Pluske et al., 1998). Both latter points are expected to reduce litter weight gain per kg increase in feed intake at higher levels or litter size. This indicates that, in fact, relatively more feed is partitioned into milk at a higher level of litter size.

The number of piglets born alive per litter was on average 10.9 for sows of mixed parity in The Netherlands in 1998 (Siva, 1999). It is well recognized that first parity sows have smaller litters than higher parity sows (e.g., Kenney and Moxley, 1978). At current levels of litter size, a higher feed intake during lactation would reduce backfat and weight losses of primiparous sows and decrease the probability of a prolonged weaning-to-estrus interval.

Implications

This study demonstrated that nursing a large litter has negative effects on lactation and post-weaning performance of primiparous sows. A greater feed intake during lactation prevents, at least partly, negative effects of nursing a large litter during lactation. Selection for a larger feed intake during lactation in combination with selection for other production and reproduction traits is, therefore, recommended especially if litter size continues to increase in the future. Moreover, it is recommended to improve environment and diet factors to prevent sows suffering from heat stress at high levels of litter size.

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8 General Discussion

Introduction

The future competitiveness of pork in the food market depends on continued genetic improvement in the efficiency of piglet production and production of quality lean pork (Clutter and Brascamp, 1998). In the past, the major part of selection pressure in pig breeding programs was directed towards improvement of lean growth efficiency by selection for particularly daily gain, feed efficiency and leanness. However, breeding objectives have begun to change, particularly over the last 10-20 years. Ollivier (1998) has presented past, present and expected future trends in breeding objectives and stated that traits such as feed intake capacity, meat quality, and various components of the sow's reproductive ability are likely to receive more and more attention. Three factors that contributed to these trends in breeding objectives are described below.

Firstly, the improvement of lean growth efficiency has been achieved largely by improved partitioning of energy away from fat deposition towards lean deposition (e.g., Kennedy et al., 1996). It is generally agreed that optimum fatness with regard to meat quality will be reached in the near future in modern genotypes, if not already reached by now (e.g., Ollivier et al., 1990; Ducos and Bidanel, 1996; Knap and Luiting, 1999). This means that the future importance of leanness in the overall breeding objective is decreasing, making the improvement of other traits economically more attractive (Ollivier et al., 1990; Haley, 1991). Feed intake capacity during growth will become more important, as future genetic progress in efficiency will be realized by a reduction of total maintenance requirements through faster growth rather than by a further reduction of fatness (i.e. reducing the proportion of feed used for maintenance).

Secondly, the use of powerful across-herd genetic evaluation techniques based on Best Linear Unbiased Prediction (BLUP) methodology has given geneticists the opportunity to substantially increase the efficiency of selection for less heritable traits like litter size. For a sustainable production, this increase in litter size, and consequently in energy and nutrients requirements of sows during lactation, should be accompanied by an increase in lactation feed intake capacity.

Thirdly, it is recognized by breeding organizations that animals must possess adequate structural soundness and the ability to cope with stresses of the production system in order to realize their genetic potential for production and reproduction (Clutter and Brascamp, 1998) and in order to produce pork in a manner that is acceptable for society. This is also supported by Knap and Luiting (1999) who stated that there seems to be a clear demand in the industry for robust dam line products that are not constrained by either limited body reserves or limited feed intake capacity.

Consequently, dam line breeding will be moving more towards reproduction performance with less emphasis on production performance. This is in line with the conclusion of Ducos and Bidanel (1996) that a selection objective that leads to an improvement in the prolificacy and to a decrease in the adiposity of the carcasses, will finally lead to increased genetic antagonism between production and reproduction traits. These findings and changes in the European carcass payment rules, indeed led to an important decrease in the economic weight of the lean content as an objective in European dam line breeds.

Feed intake capacity

Feed intake capacity is the central topic of this thesis. The series of studies presented focus on feed intake capacity of both growing pigs and lactating sows. Ad libitum feed intake is studied in relation with production and reproduction traits in order to develop breeding strategies for feed intake capacity in dam and sire lines. From a production point of view (growing pigs; Chapter 5), it is recommended to increase ad libitum feed intake during the entire growth period as feed intake capacity was lower than, or close to optimum, particularly for end product gilts. From a reproduction point of view (lactating sows; Chapters 6 and 7), it is concluded that feed intake capacity should be increased,

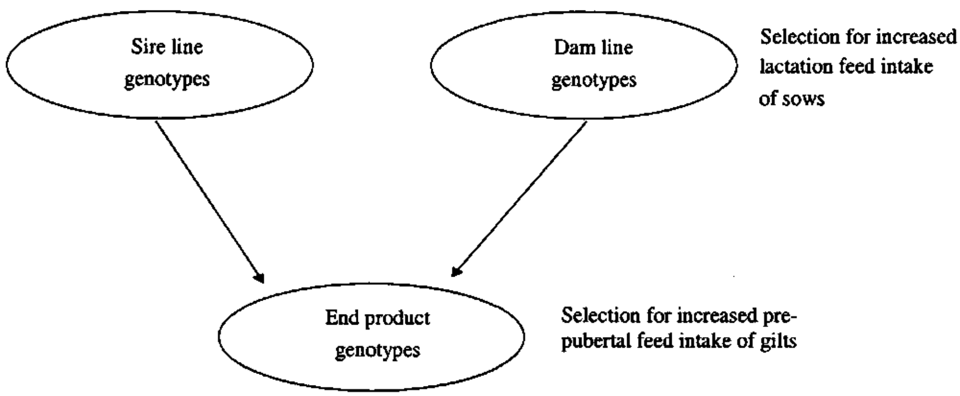

Figure 1. Desired changes in feed intake capacity during lactation (dam line genotypes) and during the growth period (end product genotypes).

especially if litter size, and consequently energy and nutrient requirements of the lactating sow, continue to increase in the future. Figure 1 presents graphically the desired changes in feed intake capacity. Implications of the desired changes for selection in dam and sire lines of pigs will be discussed in the following part.

Breeding for feed intake capacity in dam lines

The implications of the desired increase in feed intake capacity for dam lines are discussed from a reproduction point of view (i.e. feed intake capacity during lactation) because of the increasing importance of reproduction performance in dam line breeding. Next, consequences of suggested changes during lactation for production performance are discussed. To avoid overlap, implications of the desired increase in feed intake capacity from a production point of view (i.e. feed intake capacity during the growth phase) are discussed only under implications for sire lines. The example below illustrates that increasing feed intake capacity of lactating sows should be taken seriously when litter size increases further in the future.

According to Rothschild and Bidanel (1998), annual genetic trends of + .1 to .3 piglets per litter have been obtained in some dam line populations over the last couple of years. An increase of .2 piglets per year demands an annual increase in daily feed intake of the sow during lactation of 90 g, to keep track with the general rule of thumb that a sow needs 1.8 kg / d plus .45 kg / piglet / d (Koketsu et al., 1996). Assuming a current average daily feed intake during lactation of primiparous sows of about 4.8 kg (Chapter 7), an increase of 90 g means a yearly increase of 1.9%, which will be difficult to realize genetically. This is in line with results presented by Van Arendonk et al. (1991) who stated that the correlated response in roughage intake in dairy heifers is not large enough to cover the additional requirements due to increased production, when selection is on production only.

In practice, an increase in litter size is usually accompanied by a decrease in birth weight of piglets and, as a consequence, by a lower weight gain per piglet during lactation. This means that a yearly increase of somewhat less than 90 g may be sufficient. However, it is clear that changes in genetic potential for litter size should also be accompanied by improvements in the production environment that is supposed to support it (Knap and Luiting, 1999). One of the main environmental limitations on lactation feed intake of sows is the relatively high temperature in the farrowing crates, which is usually a compromise between sow and piglet requirements (Makking and Schrama, 1998). Several methods that may be used to enable heat stressed sows to dissipate (more) heat (= increase feed intake) have been summarized by Makking and Schrama (1998); using drip cooling, snout coolers or changing floor types / materials are some of the possibilities. Also feeding high-energy lactation diets (with higher fat levels, and / or lower fiber or crude protein levels) may improve energy intake, however beneficial effects through nutritional measures are expected to be less (Black et al., 1993).

Feed intake capacity during lactation may be increased genetically by including lactation feed intake capacity in the breeding goal and selection index (direct selection) or by including lactation feed intake capacity only in the breeding goal (indirect selection). Direct selection requires recording of ad libitum feed intake during lactation. This is an expensive trait to measure for the usually individually housed sows during lactation, especially compared with other traits related to reproduction like litter size and litter weight at birth and weaning, changes in body weight and backfat of the sow during lactation, and interval from weaning to first estrus. The most suitable way of increasing lactation feed intake capacity seems, therefore, to be by indirect selection. Candidate traits to increase feed intake capacity indirectly are, for example, backfat and body weight losses during lactation and interval weaning-first-estrus: backfat and body weight losses were negatively associated with feed intake during lactation, and a higher feed intake resulted in a lower probability of a prolonged interval weaning-first-estrus (Chapter 7). The interval from weaning-estrus is currently used in pig breeding programs (Knap, 1990) which may increase lactation feed intake capacity because a prolonged interval has a negative effect on the reproductive breeding value of sows and boars.

Indirect selection for feed intake capacity during lactation may also be accomplished via pre-pubertal production traits. Most suitable candidate traits are average daily gain and daily feed intake capacity, keeping in mind that dam line breeding should be moved away from breeding for leanness. An advantage of the recording of pre-pubertal traits is that data of more animals can be recorded (not sex-limited) and data may also be recorded for gilts that have no lactation. Moreover, the early-age of measurement may help to select candidate parents at an early stage. A major condition for the recording of those pre-pubertal traits is that animals must be fed ad libitum up to for example 85-100 kg of body weight, which is not common practice for dam line gilts. The recording of pre-pubertal daily feed intake capacity requires investments in computerized feeding stations, which again makes it a relatively expensive trait to measure.

Successful application of indirect selection depends on the genetic correlations between lactation feed intake capacity and the above mentioned candidate traits for selection. There is a lack of information concerning genetic parameters for feed intake capacity during lactation. Van Erp et al. (1998) estimated a heritability of .19 for lactation feed intake capacity and a genetic correlation between feed intake capacities during growth and lactation of .92 (± .5) in a small data set. Estimates of genetic correlations between pre-pubertal feed intake and daily gain generally range from .6 to .9 (e.g., Chapter 4; Von Felde et al., 1996; Labroue et al., 1997). This may suggest a positive genetic association between pre-pubertal daily gain and lactation feed intake capacity.

However, much of the evidence for carry-over effects of pre-pubertal traits to lactation feed intake capacity is anecdotal, and is awaiting proper genetic confirmation (Knap and Luiting, 1999). In fact, the same is true for relationships between lactation feed intake capacity and mentioned reproduction trait candidates.

In combination with indirect selection for lactation feed intake capacity, circumstances during the first lactation could be aggravated for breeding sows to force these sows to express their full genetic potential for reproduction. Circumstances may be aggravated for example by standardizing litter size during lactation to 12 or 13 piglets, by using low energy feeds, by giving no creep feed to piglets, and / or by increasing the temperature in the farrowing crates. Choosing for such a strategy, however, may result in a reduction of selection intensity if test capacity is not expanded, as the culling of animals due to a.o. reproductive failures will be higher. Furthermore, increased culling of sows and reduced growth of piglets (Chapter 7) will increase costs.

In summary, the best way of genetically increasing lactation feed intake capacity seems to be by indirect selection, possibly in combination with an aggravation of test circumstances. Which traits may be used best to increase lactation feed intake capacity indirectly will mainly depend on genetic relationships among the various traits and additional costs of recording the required data.

Consequences for feed intake capacity and optimum feed intake of growing pigs

Starting point for this paragraph is the assumption that feed intake capacity of lactating sows is going to increase in the future. Though the genetic relationship between lactation feed intake capacity and production performance is awaiting for proper confirmation, it seems likely that traits like pre-pubertal feed intake capacity and daily gain will increase as a result of an increase in lactation feed intake capacity. Based on genetic relationships among pre-pubertal ad libitum feed intake, daily gain, and lean content (Chapter 4), one would expect a decrease in lean content, rather than an increase, due to an increase in lactation feed intake capacity. Kanis and De Vries (1992) studied optimum selection directions for feed intake capacity of growing pigs by means of simulation, using the linear plateau concept model. They showed that when selection was for both pre-pubertal feed intake capacity and for daily gain with little emphasis on leanness, feed intake capacity was increasing at a faster rate than optimum feed intake. An increase in pre-pubertal feed intake capacity in dam line genotypes will be passed on to end product genotypes (Figure 1). As a consequence, the desired increase in feed intake capacity of end product growing pigs (Chapter 5) will be accomplished at least partly via dam line breeding.

Breeding for feed intake capacity in sire lines

Financial returns from breeding largely result from the end product pig. Therefore, the optimum feed intake capacity in the growing pig has to be defined on the level of the end product pig. However, selection of pigs is performed in the purebred lines. As a consequence, selection for production traits in the purebred lines has to be balanced in such a way that the optimum feed intake is achieved in the end product pig. On the base of linear plateau relationships between protein deposition and feed intake of end product genotype pigs (Chapter 5), it was recommended to increase feed intake capacity during the entire growth period. As discussed above, future selection procedures in dam line breeding will increase feed intake capacity of end product growing pigs, which diminishes the need to increase feed intake capacity via selection in sire lines.

Kanis and De Vries (1992) developed selection indices using the linear plateau concept in order to optimize selection for feed intake capacity in growing pigs. For the situation where feed intake capacity is close to optimum, the breeding goal should be primarily to improve the protein deposition per unit increase in feed intake (= slope PD; see Chapter 5) and to improve maximum protein deposition. Feed intake capacity should remain in the optimum (actual economic value for feed intake capacity equals 0 in the optimum). Selection for slope PD will result in leaner carcasses. When optimum fat levels have been reached in the end product pig, selection should focus more on maximum protein deposition only. However, traits like slope PD and maximum protein deposition are not measured in practice. The key to selection in sire lines is, therefore, to find the optimum balance between selection for carcass leanness, daily gain and feed intake in order to achieve the optimum feed intake in the end product pig. (Kanis and De Vries, 1992).

The development of computerized feeding stations enabled the recording of ad libitum feed intake of group-housed growing pigs. This brings forward the question whether or not breeding organizations should invest in these stations in order to measure ad libitum feed intake. Actual recording of ad libitum feed intake of potential breeding animals may add 2 to 36% to the rate of genetic improvement in efficient lean tissue growth rate, depending on genetic parameter estimates and economic values (calculations based on information presented in Chapter 4; De Haer, 1992; Hall et al., 1998, 1999b). Inclusion of traits in the index describing the course of feed intake capacity (e.g., intercept or slope of a linear fit to feed intake per day records) resulted in a small increase (0 - 7 %) in accuracy of selection (Chapter 4). Feed intake behavior traits (e.g., number of visits and total visiting time per day) that are recorded in addition to average daily feed intake are also heritable, but generally show low to moderate genetic correlations with production traits (e.g., Von Felde et al., 1996; Labroue et al., 1997). The potential of these traits for improving the accuracy of selection seems to be limited, though Hall et al. (1999a) estimated higher genetic correlations between behavior and production traits than the other authors, resulting in a substantial increase in accuracy of selection (+ 11-13%; Hall et al., 1998, 1999b).

Computerized recordings of individual feed intake traits are much more expensive than recordings of traits like daily gain and backfat thickness (Webb, 1997). The cost of feed intake recording per pig will decrease when the efficiency of the use of feeding stations is increased. There are several ways to increase the efficiency. Firstly, by using computerized methods to check recorded data for errors and to summarize data per visit to the desired traits (e.g., average daily feed intake during the test period), labor costs will be reduced (Chapter 2 and 3). Secondly, it is sufficient to record feed intake during only part of the test period (e.g., every second week; Chapter 3) to end up with an accurate record for average daily feed intake. Thirdly, Von Felde et al. (1996) and Hall et al. (1999a) showed that the genetic variation of feed intake varies during the test period (genetic variation is not constant over time). By recording feed intake data only during the most informative period (largest h^2), feeding stations may be used more efficiently and selection can even lead to a higher response than using the average daily feed intake over the entire test period (Von Felde et al., 1996). Hall et al. (1999b) studied the effect of recording feed intake during only a part of the test period (during only two weeks of an eight weeks test period) and found about 12% loss in accuracy compared with recording feed intake data during the entire test period.

The question whether a breeding organization should invest in computerized feeding stations is first of all an economic question, i.e. a comparison of benefits and costs. In literature, no references were found that compared financial benefits and costs. Cameron (1998) concluded that it was not necessary to record feed intake (based on data from experiments) as selection for lean growth rate was preferred above selection for efficiency of lean growth. In addition to the financial argument, it seems justified to invest in a number of feeding stations in order to monitor feed intake capacity of growing pigs. In highly productive pig genotypes, fitness may become compromised directly, by a gradually impaired development of supportive organs and tissues, or indirectly, when production-related processes come to demand so many resources from the animal that functions such as immune response and coping with other stressors become resource limited (Knap and Luiting, 1999). Breeding programs for broiler chickens have achieved greater genetic change in the production-related breeding objectives than pig breeding programs. As a consequence, the poultry sector has been confronted earlier and more seriously with fitness constraints than the pig sector (Scheele, 1996; Knap and Luiting, 1999). In commercial pig breeding programs, selection limits have not been reached yet (Merks, 1999) but it is important to avoid fitness constraints occurring in the pig sector, both from ethical / animal welfare and economic point of view. Only improved production levels without effect on health or metabolic balance of the animal seem to be accepted by society (Merks, 1999). Although feed intake capacity is only one of the factors that contribute to metabolic balance of animals, it seems justified to monitor it because of the multi-sided character of this trait.

Level of optimum feed intake capacity

In the present study, the economical optimum feed intake has been defined as the minimum feed intake to reach the maximum protein deposition (i.e. feed intake at the breakpoint) as suggested by Kanis and De Vries (1992) and Schinkel and De Lange (1996). The exact position of the economic optimum feed intake depends on costs and prices of production. For example, optimum feed intake capacity may be lower than the breakpoint when carcass lean percentage has a large effect on the profit. On the other hand, it may be necessary to feed animals at a level higher than the breakpoint as a minimum amount of fat in the carcass is likely necessary to guarantee sufficient meat quality (Kanis and De Vries, 1992). The latter may also be true when daily gain is important, for example to reduce housing costs per pig.

Main conclusions

From this thesis (combined with some related studies), the following main conclusions can be drawn for future pig breeding programs:

- Feed intake capacity during lactation should be increased, especially because litter size, and consequently energy and nutrient requirements of the sow, continue to increase in the future. The most suitable way of genetically increasing lactation feed intake capacity in dam line genotypes seems to be by indirect selection, possibly in combination with an aggravation of lactation circumstances.
- Feed intake capacity during the entire growth period should be increased as feed intake capacity is lower than or close to optimum particularly for end product gilts. This

increase will be accomplished, at least partly, via future dam line selection for feed intake capacity during lactation, which diminishes the need to increase feed intake capacity via selection in sire lines.

- The efficiency of the use of feeding stations will be increased by using computerized methods to check recorded data for errors and to summarize data per visit to the desired traits (e.g., average daily feed intake during the test period). Furthermore, it is sufficient to record feed intake during only parts of the test period (e.g., every second week) to end up with an accurate record for average daily feed intake. Inclusion of traits in the index describing the course of feed intake capacity results in a small increase in accuracy of selection. The question whether a breeding organization should invest in computerized feeding stations is primarily an economic question. However, it seems justified to invest in a number of feeding stations in order to monitor feed intake capacity of growing pigs.

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Summary

This thesis deals with feed intake capacity of pigs. By selection, breeding organizations try to achieve genetic improvement in production and reproduction efficiency. Future genetic improvement may become constrained by a limited feed intake capacity of growing pigs and lactating sows, respectively. The aim of this thesis is to study the actual feed intake capacity of growing pigs and lactating sows in relation to their potential for production and reproduction in order to get a better understanding and to develop breeding strategies for feed intake capacity in dam and sire lines. Furthermore, the use of computerized feeding stations (i.e. feeding stations that are used for the recording of feed intake of group-housed growing pigs) is evaluated in order to reduce costs of recording feed intake and to increase benefits of investing in feeding stations for breeding organizations.

Computerized feeding stations

Chapter 2 describes algorithms to identify errors in feed intake data of growing pigs recorded with computerized feeding stations. The numbers of errors need to be kept small, as it is impossible to adjust feed intake data without bias and adjusting data is time consuming and, consequently, expensive. The objective of this study was to develop algorithms to monitor the operation of feeding stations, by frequently checking recorded feed intake data for errors. Results indicated several instances where feeding stations functioned sub-optimally during a period of days or weeks. Frequent checking and correction of the functioning of a feeding station would, therefore, reduce the incidence of errors. Expanding a feeding station's software with the editing system described in Chapter 2 will allow a daily check for errors of recorded data.

Computerized feeding stations record data of each visit to the station, which means that a large number of feed intake traits can be derived per pig. In practice, average daily feed intake during the test period (from 25 to 110 kg) is the only information systematically used by pig breeding organizations. Average daily feed intake is usually computed after adjustments for errors in the recorded data. Instead of adjusting, it might be better to eliminate incorrect daily feed intake records and to consider these as missing values. The objective of Chapter 3 was to study the effect of such missing values on the

estimate of average daily feed intake during the test period. In this study, average daily feed intake was estimated by fitting curves to the feed intake data per pig. Results indicated that pigs can have missing values for up 70% of the test days (randomly spread over the test period) and still end up with an accurate estimate of average daily feed intake. This implies that considering incorrect feed intake per day records as missing is a good alternative for adjusting incorrect data. Moreover, the use of functions to estimate average daily feed intake enables a more efficient use of feeding stations by recording feed intake data during only parts of the test period.

The fit of a linear regression to daily feed intake records results per pig in a record for intercept (feed intake at the start of the test period), slope (increase during the test period), and residual standard deviation of the fit. Genetic aspects of these traits were studied in Chapter 4. Heritabilities estimated for intercept, slope, and residual standard deviation were .32, .32, and .46, respectively. Genetic correlations of these characteristics with performance and carcass traits ranged from .12 to .17 for feed conversion ratio, .36 to .75 for daily gain, and -.61 to .25 for lean content. The intercept seems the most promising candidate to improve the selection for an efficient lean growth as it was positively correlated with both average daily gain and lean content.

Feed intake capacity in relation to production and reproduction performance

For pig breeding organizations, it is important that end product growing pigs have a feed intake capacity that is close to their economic optimum. An experiment was set up to elucidate the desirable direction of selection for feed intake capacity of growing pigs (Chapter 5). A linear plateau relationship between protein deposition and feed intake was assumed to derive the optimum feed intake for the early (25-65 kg), middle (65-95 kg), and late phase (95-125 kg) of the growing period, separately. Actual feed intake capacity was below the optimum more often for gilts and boars than for castrates (within genotype), and more often for end product genotypes than for dam line genotypes. Feed intake capacity of end product gilts was below or close to optimum during the total growing period from 25-125 kg. Results indicated that it may be beneficial to select for a higher ad libitum feed intake in combination with selection for other production traits.

Chapters 6 and 7 deal with feed intake capacity of lactating sows. In Chapter 6, it is argued on base of a literature study that voluntary feed intake of lactating sows should be increased by selection, especially if litter size, and consequently energy and nutrient requirements of sows continue to increase. The objective of the experiment described in Chapter 7 was to investigate whether nursing a large number of piglets has negative effects on lactation and post-weaning performance of primiparous sows and if a greater lactation feed intake can prevent these possible negative effects. Sows nursing a large litter during lactation had a feed intake similar as sows nursing a small litter, however, mobilized more body tissues and had a higher probability of a prolonged weaning-to-estrus interval. A higher daily feed intake during lactation (for a given litter size) reduced tissue losses of the sow and reduced the probability of a prolonged weaning-to-estrus interval. There were some indications that sows nursing a large litter may suffer more often from heat stress than sows nursing small litters. It is therefore not only recommended to increase lactation feed intake by selection but also to simultaneously improve environmental and dietal factors to reduce occurrence of heat stress.

Breeding for feed intake capacity in dam and sire lines

In sire lines, selection is mainly for production traits, whereas selection in dam lines is for production as well as for reproduction traits. Due to several tendencies in pig breeding, the relative importance of reproduction performance in future dam line breeding will increase compared to production performance. Therefore, the implications of the desired increase in feed intake capacity for dam line breeding are discussed from a reproduction point of view.

Lactation feed intake capacity may be increased genetically by including lactation feed intake in the breeding goal and selection index (direct selection) or by including lactation feed intake only in the breeding goal (indirect selection). Direct selection requires recording of ad libitum feed intake during lactation, which is an expensive trait to measure. The most suitable way of increasing lactation feed intake seems therefore to be by indirect selection, possibly in combination with an aggravation of test circumstances for potential breeding sows (for example by standardizing litter size during lactation to 12 or 13 piglets). The latter would force sows to express their full genetic potential for reproduction. Candidate traits that can be used in a selection index to increase lactation feed intake by indirect selection are for example backfat and body weight losses during lactation, interval weaning-first-estrus, and pre-pubertal feed intake and daily gain. Which traits may be used best will mainly depend on genetic relationships among the various traits and lactation feed intake, and on additional costs of recording the required data.

Though genetic relationships between lactation feed intake and production performance still have to be established, it seems likely that traits like pre-pubertal daily feed intake and daily gain will also increase when lactation feed intake increases. An increase in pre-pubertal feed intake capacity in dam line genotypes will be passed on to end product genotypes. This means that the desired increase in feed intake capacity of end product growing pigs will likely be accomplished at least partly via dam line breeding, which diminishes the need to increase feed intake capacity via selection in sire lines. For sire lines, the key to selection is to find the optimum balance between selection for carcass leanness, daily gain and feed intake in order to achieve the optimum feed intake in the end product pig.

The development of computerized feeding stations brings forward the question whether or not breeding organizations should invest in these stations. This is first of all an economic question, i.e. a comparison of costs and benefits for selection. However, it seems justified to invest in feeding stations in order to monitor feed intake capacity of growing pigs.

Main conclusions

From this thesis (combined with some related studies), the following main conclusions can be drawn for future pig breeding programs:

- Feed intake capacity during lactation should be increased, especially because litter size, and consequently energy and nutrient requirements of the sow, continue to increase in the future. The most suitable way of genetically increasing lactation feed intake capacity in dam line genotypes seems to be by indirect selection, possibly in combination with an aggravation of lactation circumstances.
- Feed intake capacity during the entire growth period should be increased as feed intake capacity is lower than or close to optimum particularly for end product gilts. This increase will be accomplished, at least partly, via future dam line selection for feed intake capacity during lactation, which diminishes the need to increase feed intake capacity via selection in sire lines.
- The efficiency of the use of feeding stations will be increased by using computerized methods to check recorded data for errors and to summarize data per visit to the desired traits (e.g., average daily feed intake during the test period). Furthermore, it is sufficient to record feed intake during only parts of the test period (e.g., every second week) to end up with an accurate record for average daily feed intake. Inclusion of traits in the index describing the course of feed intake capacity results in a small increase in accuracy of selection. The question whether a breeding organization should invest in computerized feeding stations is primarily an economic question. However, it seems justified to invest in a number of feeding stations in order to monitor feed intake capacity of growing pigs.

Samenvatting

In dit proefschrift staat voeropnamecapaciteit van varkens centraal. Fokkerijorganisaties proberen door selectie genetische vooruitgang te behalen in productie- en reproductie-efficiëntie. Toekomstige genetische vooruitgang zou beperkt kunnen zijn doordat de voeropnamecapaciteit van vleesvarkens en lacterende zeugen tekort schiet. De doelstelling van dit proefschrift is om de huidige opnamecapaciteit van vleesvarkens en lacterende zeugen te bestuderen in relatie tot hun aanleg voor productie en reproductie om, op basis van verworven inzichten, fokkerijstrategieën omtrent voeropnamecapaciteit in zeugen- en berenlijnen te ontwikkelen. Verder wordt het gebruik van geautomatiseerde voerstations (= voerstations om individuele voeropnamegegevens van in groepen gehuisveste vleesvarkens te verzamelen) bestudeerd met als doel de kosten van voeropnameregistratie te verlagen en de baten van het investeren in voerstations voor fokkerijorganisaties te verhogen.

Geautomatiseerde voerstations

Hoofdstuk 2 beschrijft algoritmen voor het opsporen van fouten in voeropnamegegevens van vleesvarkens, verzameld met geautomatiseerde IVOG®-voerstations. Het aantal fouten dient zo laag mogelijk te worden gehouden, omdat eenmaal opgetreden fouten doorgaans niet volledig juist gecorrigeerd kunnen worden en omdat corrigeren van gegevens een tijdrovende en daardoor dure bezigheid is. De doelstelling van deze studie was het ontwikkelen van algoritmen om het functioneren van voerstations te monitoren door frequent de verzamelde gegevens te controleren op fouten. Uit de resultaten bleek dat het herhaaldelijk voorkwam dat voerstations gedurende meerdere dagen of weken sub-optimaal functioneerden. Frequent controleren en corrigeren van het functioneren van voerstations zal daarom de incidentie van fouten verlagen. Een uitbreiding van de software van voerstations met de binnen dit hoofdstuk beschreven algoritmen maakt een dagelijkse controle van verzamelde gegevens mogelijk.

Geautomatiseerde voerstations leggen gegevens vast van ieder bezoek aan het station. Dit betekent dat er per varken een veelheid aan voeropnamekenmerken kan worden afgeleid. Momenteel wordt door fokkerijorganisaties alleen de gemiddelde voeropname gedurende de testperiode (van ca 25 tot 110 kg) systematisch gebruikt. De gemiddelde dagelijkse voeropname wordt doorgaans berekend nadat de foute gegevens zo goed mogelijk zijn gecorrigeerd. In plaats van corrigeren is het misschien beter onjuiste gegevens over voeropname per dag te elimineren (beschouwen als ontbrekende waarden) en niet mee te nemen in de berekening van de gemiddelde voeropname. De doelstelling van Hoofdstuk 3 was het effect van zulke ontbrekende waarden op de schatting van gemiddelde voeropname gedurende de testperiode te bestuderen. In deze studie is de gemiddelde voeropname geschat door curves te fitten door de dagelijkse voeropnamegegevens per dier. De resultaten gaven aan dat een varken willekeurig verdeeld over de testperiode voor maximaal 70% van de testdagen een ontbrekende waarde mag hebben om toch op een nauwkeurige schatting voor gemiddelde voeropname uit te komen. Dit betekent dat het als ontbrekend beschouwen van foute voeropnames per dag een goed alternatief is voor het corrigeren van fouten. Daarnaast maakt het gebruik van functies voor het schatten van de gemiddelde voeropname het mogelijk om voerstations efficiënter te gebruiken door bijvoorbeeld slechts gedurende bepaalde delen van de testperiode voeropnamegegevens te verzamelen.

Het fitten van een rechte lijn door de voeropnames per dag geeft voor ieder dier een waarde voor de voeropnamekenmerken intercept (voeropname aan begin testperiode), helling (toename gedurende de testperiode) en residuele standaarddeviatie van de fit. De genetische aspecten van deze kenmerken zijn in Hoofdstuk 4 bestudeerd. De geschatte erfelijkheidsgraden voor intercept, helling en residuele standaard deviatie waren respectievelijk 0,32, 0,32 en 0,46. Genetische correlaties van deze kenmerken met mest- en slachteigenschappen liepen uiteen van 0,12 tot 0,17 voor voederconversie, van 0,36 tot 0,75 voor groei en van –0,61 tot 0,25 voor vleespercentage. De intercept lijkt het meest geschikte kenmerk om op te nemen in het fokprogramma om de genetische vooruitgang van mest- en slachteigenschappen verder te verhogen omdat dit kenmerk positief gecorreleerd is met zowel groei als vleespercentage.

Voeropnamecapaciteit in relatie tot prestaties voor productie en reproductie

Het is voor fokkerijorganisaties belangrijk dat commerciële vleesvarkens (eindproducten) een voeropnamecapaciteit hebben op of nabij hun economisch optimum. Er is een experiment uitgevoerd met als doel de gewenste selectierichting voor voeropnamecapaciteit (hoger of lager) voor vleesvarkens te bepalen (Hoofdstuk 5). De optimale voeropname capaciteit is bepaald voor de vroege (25-65 kg), middelste (65-95 kg), en late fase (95-125 kg) van de groeiperiode. Hierbij is een lineair-plateau relatie verondersteld tussen eiwitaanzet en voeropname. Gelten en beren hadden vaker een voeropnamecapaciteit onder het optimum dan borgen (binnen genotype) en eindproductgenotypen vaker dan zeugenlijngenotypen. Gedurende de volledige periode van 25-125 kg was de voeropnamecapaciteit van eindproductgelten lager dan, of gelijk aan, het optimum. Het lijkt daarom gewenst om op een hogere voeropnamecapaciteit te selecteren.

Hoofdstukken 6 en 7 zijn gericht op voeropnamecapaciteit van lacterende zeugen. In Hoofdstuk 6 wordt op basis van een literatuurstudie betoogd dat de voeropname van lacterende zeugen verhoogd zou moeten worden door selectie, met name wanneer toomgrootte blijft toenemen, en als gevolg daarvan ook de energie- en nutriëntenbehoefte van zeugen. Het doel van de in Hoofdstuk 7 beschreven studie was na te gaan of het zogen van een grote toom negatieve gevolgen heeft voor de prestaties van eerste worpszeugen tijdens en na de lactatie, en of een hogere voeropname deze mogelijke negatieve effecten kan voorkomen. Zeugen die een grote toom zoogden, hadden een voeropname die ongeveer even groot was als die van zeugen met een kleine toom, maar mobiliseerden meer lichaamsweefsel en hadden een grotere kans op een verlengd interval spenen-bronst. Een hogere voeropname tijdens de lactatie (bij een bepaalde toomgrootte) verlaagde de mobilisatie van lichaamsweefsels en verkleinde de kans op een verlengd interval. Er waren aanwijzingen dat zeugen die een grote toom zoogden meer last hadden van warmtestress dan zeugen met een kleine toom, waardoor de voeropname wordt beperkt. Daarom wordt aanbevolen om naast selectie op een hogere voeropname ook milieu- en voerfactoren te verbeteren om het optreden van warmtestress zoveel mogelijk te voorkomen.

Fokken op voeropnamecapaciteit in zeugen- en berenlijnen

In berenlijnen wordt hoofdzakelijk op productiekenmerken geselecteerd terwijl in zeugenlijnen op productie- en vooral reproductiekenmerken wordt geselecteerd. Door diverse ontwikkelingen in de varkensfokkerij zal het relatieve belang van reproductie binnen zeugenlijnen toenemen. Daarom is de discussie over de gewenste toename in voeropnamecapaciteit door selectie in zeugenlijnen opgezet vanuit het oogpunt van reproductie (=voeropnamecapaciteit tijdens de lactatie).

De voeropnamecapaciteit tijdens de lactatie kan genetisch worden verhoogd door voeropname zowel in het fokdoel als in de index op te nemen (directe selectie) of door voeropname alleen in het fokdoel op te nemen (indirecte selectie). Directe selectie vereist registratie van voeropname tijdens de lactatie, wat duur is. Voeropname verhogen via indirecte selectie lijkt daarom aantrekkelijker, mogelijk in combinatie met een verzwaring van de lactatieomstandigheden voor potentiële fokzeugen (bijvoorbeeld toomgrootte tijdens lactatie verhogen naar 12 of 13 biggen). Dit laatste dwingt zeugen om hun volledige genetische potentieel voor reproductie tot expressie te brengen. Kandidaatkenmerken om via indirecte selectie de voeropnamecapaciteit tijdens de lactatie te verhogen zijn bijvoorbeeld het verlies van spekdikte en gewicht tijdens de lactatie, het interval spenen-bronst en voeropname en groei tijdens de groeiperiode. Welke kenmerken het best gebruikt kunnen worden zal met name afhangen van genetische relaties tussen de kandidaat selectiekenmerken en voeropname tijdens de lactatie en van bijkomende kosten van het registreren van betreffende kenmerken.

Selectie gericht op een hogere voeropname tijdens de lactatie zal waarschijnlijk resulteren in een hogere gemiddelde voeropname en groei tijdens de testperiode. Een toename in de voeropnamecapaciteit tijdens de groeiperiode bij varkens van zeugenlijnen zal worden doorgegeven aan het eindproduct. Dit betekent dat de gewenste toename in voeropnamecapaciteit tijdens de groeiperiode voor eindproductvarkens in ieder geval ten dele wordt bewerkstelligd door selectie op voeropnamecapaciteit tijdens de lactatie binnen zeugenlijnen. Dit maakt selectie op een hogere voeropname binnen berenlijnen minder noodzakelijk. Voor selectie binnen berenlijnen is het zaak de optimale balans te vinden tussen selectie op bevleesdheid, groei en voeropname teneinde de voeropnamecapaciteit van eindproductvarkens optimaal te laten zijn.

De ontwikkeling van geautomatiseerde voerstations brengt de vraag met zich mee of fokkerijorganisaties zouden moeten investeren in deze stations. Dit is ten eerste een economische vraag, dat wil zeggen een afweging van kosten en baten ten behoeve van selectie. Het lijkt echter nuttig om te investeren in voerstations om de voeropname van vleesvarkens te kunnen monitoren.

Belangrijkste conclusies

De belangrijkste conclusies van dit proefschrift (en van hieraan gerelateerde studies) voor toekomstige varkensfokprogramma's zijn:

- Voeropnamecapaciteit tijdens de lactatie dient te worden verhoogd, met name omdat toomgrootte, en als gevolg hiervan de energie- en nutriëntenbehoefte van zeugen in de toekomst zal blijven toenemen. De meest geschikte manier om voeropnamecapaciteit in zeugenlijnen te verhogen lijkt indirecte selectie, mogelijk in combinatie met een verzwaring van omstandigheden tijdens de lactatie.
- Voeropnamecapaciteit gedurende de groeiperiode dient te worden verhoogd omdat de huidige voeropnamecapaciteit van eindproductgelten lager is dan, of gelijk aan, het

optimum. De gewenste toename zal in ieder geval ten dele worden bereikt via toekomstige selectie binnen zeugenlijnen op voeropnamecapaciteit tijdens de lactatie. Dit maakt selectie op een hogere voeropname in berenlijnen vooralsnog minder noodzakelijk.

- De efficiëntie van het gebruik van voerstations kan verhoogd worden door gebruik te maken van geautomatiseerde methoden voor het controleren van voeropnamegegevens op fouten en bij het omzetten van voeropnamegegevens naar de gewenste kenmerken (bijvoorbeeld gemiddelde voeropname tijdens de testperiode). Het is daarnaast voldoende om voeropnamegegevens alleen tijdens delen van de testperiode (bijvoorbeeld om de andere week) te verzamelen om toch tot een nauwkeurige schatting van de gemiddelde voeropname tijdens de testperiode te komen. Het opnemen van kenmerken die het verloop van voeropname gedurende de testperiode beschrijven in de index gaf een kleine toename in genetische vooruitgang. De vraag of fokkerijorganisaties zouden moeten investeren in geautomatiseerde voerstations is ten eerste een economische afweging. Het lijkt echter nuttig om te investeren in voerstations om de voeropname van vleesvarkens te monitoren.

Nawoord

Het in dit proefschrift beschreven onderzoek is uitgevoerd bij Leerstoelgroep Fokkerij en Genetica van Wageningen Universiteit. Door de brede opzet en de experimenten uitgevoerd voor dit onderzoek hebben velen een bijdrage geleverd aan dit proefschrift. Allen hartelijk dank hiervoor. Een aantal personen wil ik graag met name noemen. In het bijzonder zijn dit Egbert Kanis en Karel de Greef voor de dagelijkse begeleiding en Pim Brascamp, Martin Verstegen en Jan Merks die meer de grote lijnen in de gaten hielden. Zij stonden garant voor een inspirerende en wetenschappelijke begeleiding. Personen die aan onderdelen van dit project hebben meegewerkt zijn Evy Apeldoorn, Bart Ducro, Ton van Erp, Ab Groen, Adriaan de Haan, Bas Kemp, Ryan Molendijk, Bianca van der Pasch en Evert van Steenbergen. Bedankt voor de prettige samenwerking. Daarnaast wil ik Gert Hemke, Rob Krabbenborg en Jan Smulders bedanken voor de ondersteuning bij het opzetten van voor dit onderzoek uitgevoerde experimenten, en het bediscussiëren van de resultaten ervan.

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Jaco

Curriculum Vitae

Jacob Jan Eissen werd op 16 maart 1969 geboren te Radewijk (gemeente Hardenberg) en is getogen in Wanneperveen. In 1987 behaalde hij het VWO-diploma aan de Christelijke Scholengemeenschap Dingstede te Meppel. Datzelfde jaar begon hij met de studie Zoötechniek aan de toenmalige Landbouwuniversiteit te Wageningen. In juni 1993 sloot hij zijn studie af met afstudeervakken in de Veefokkerij en Bedrijfskunde. Van maart 1994 tot september 1994 werkte hij als projectmedewerker voor het Productschap voor Veevoeder en aansluitend tot mei 1995 als wetenschappelijk medewerker voor de Zoötechnische vakgroepen Veefokkerij, Veehouderij en Veevoeding van de Landbouwuniversiteit. Vanaf 1 mei 1995 was hij als Assistent in Opleiding aangesteld bij de Vakgroep Veefokkerij (thans Leerstoelgroep Fokkerij en Genetica) op het in dit proefschrift beschreven onderzoek. Sinds 1 februari 2000 werkt hij als onderzoeker bij het Breeding Research Centre van Nutreco in Boxmeer.