Ann. Zootech. 48 (1999) 247–261

Original article

Feed intake behaviour of group-housed Piétrain and Large White growing pigs

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(Received 27 May 1998; accepted 2 February 1999)

Abstract — Feed intake behaviour traits were recorded on 210 Large White and 114 Piétrain entire male pigs housed in single-breed groups (range of group size: 8–13) and having 24 h access to 'Acema 48' electronic feed dispensers. Three stages of growth were considered (average body weights of 39, 64 and 89 kg for both breeds), and feeding behaviour traits were calculated separately for two periods of the day (8–20 h and 20–8 h). Slower-growing and leaner Piétrains compared with Large Whites displayed a much lower daily feed intake level (1.72 vs. 2.12 kg, $P < 0.001$) as well as a different feed intake pattern, consisting of much less feeder visits per day (8.8 vs. 15.7, $P < 0.001$), shorter daily eating time (49.7 vs. 55.6 min, $P < 0.001$), smaller daily number (5.84 vs. 6.53, $P < 0.05$) and average size (300 vs. 332 g, $P < 0.05$) of meals, and slower rate of feed intake (34.8 vs. 38.1 g·min^{-1}, $P < 0.01$). Average time per meal (9.4 min), however, was not breed-dependent. Both breeds followed similar trends in feeding behaviour over the course of growth, even though the breed by stage of growth interaction was revealed to be significant for several traits. The nychthemeral distribution of feed intake was around 70 % and 30 % feed consumed in the 'daylight' and 'nightly' periods of day, respectively. The percentage of nightly feeding activity significantly decreased in the second part of the growth period. There were noticeable batch (season) and group size effects on most feed intake pattern traits but not on feed intake level. The latter trait showed a markedly lower repeatability across the three stages of growth (around 0.30) than the other feeding behaviour traits (0.50–0.60). This study confirms that the feed intake pattern of growing pigs is influenced by genetic and environmental effects and, to a lesser extent, by genotype x environment interaction effects. (© Elsevier / Inra)

pig / feeding behaviour / breed comparison / Piétrain / Large White

Résumé — Comportement alimentaire de porcs en croissance Piétrain et Large White élevés en groupe. À l'aide d'automates d'alimentation « Acema 48 », sept caractères de comportement alimentaire (quantité consommée et durée de consommation par jour, nombre quotidien de visites à

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l'automate et de repas, taille et durée des repas, vitesse d'ingestion) ont été étudiés chez des mâles entiers Large White ($n = 210$) et Piétrain ($n = 114$) contrôlés entre 35 et 95 kg. Les animaux étaient élevés en loges collectives monoraciales (taille du groupe variant de 8 à 13) et avaient accès 24 h sur 24 à l'automate. Trois stades de croissance (semaines de contrôle) ont été retenus pour l'analyse, avec un poids vif moyen respectivement égal à 39, 64 et 89 kg pour l'une et l'autre race. Les caractères de comportement alimentaire ont été calculés séparément pour deux périodes du nycthémère (de 8 h à 20 h et de 20 h à 8 h) afin de comparer les activités alimentaires diurnes et nocturnes. Le modèle d'analyse comportait l'effet aléatoire de l'animal intra-race et les effets fixés suivants : race, bande de contrôle (4 niveaux), taille du groupe (2 niveaux : 8–10 et 11–13), stade de croissance, période du nycthémère et plusieurs interactions à 2 ou 3 voies, impliquant notamment le facteur race. Par rapport au Large White, le Piétrain a présenté une consommation journalière d'aliment nettement plus faible (1,72 contre 2,12 kg, $p < 0,001$) et un comportement alimentaire sensiblement différent, se caractérisant par un nombre beaucoup plus faible de visites à l'automate (8,8 contre 15,7 par jour, $p < 0,001$), une durée journalière de consommation plus courte (49,7 contre 55,6 minutes, $p < 0,001$), une vitesse d'ingestion plus lente (34,8 contre 38,1 g par minute, $p < 0,001$), un nombre plus faible de repas (5,84 contre 6,53 par jour, $p < 0,05$) et une moindre taille moyenne des repas (300 contre 332 g, $p < 0,05$). En revanche, la durée moyenne des repas (9,4 min) n'a pas différé entre races. Les deux races ont montré des évolutions globalement similaires du comportement alimentaire au cours de la croissance, bien que l'interaction race × stade de croissance se soit révélée statistiquement significative pour plusieurs caractères, en particulier le nombre quotidien et la taille moyenne des repas. La répartition nycthémérale de la consommation d'aliment (en moyenne 70 et 30 % pendant les périodes diurne et nocturne) diffère assez peu entre races, et la part de l'activité alimentaire intervenant entre 20 h et 8 h s'abaisse dans la seconde partie de la période de croissance, quelle que soit la race. Des effets notables de la bande de contrôle (assimilables à des effets de la saison) ainsi que des effets de la taille du groupe ont été observés pour la plupart des composantes du comportement alimentaire (notamment la durée quotidienne de consommation et la vitesse d'ingestion), mais sans que ces deux facteurs agissent sur le niveau de consommation alimentaire. La répétabilité entre stades de croissance a été nettement plus faible pour la consommation moyenne journalière (environ 0,30) que pour les autres caractères de comportement alimentaire (0,50–0,60). Ces différences de répétabilité sont conformes à ce que l'on sait des héritabilités respectives des caractères. Cette étude confirme que le comportement alimentaire du porc en croissance (niveau d'ingestion et profil d'activité alimentaire) est influencé par des effets génétiques (ici la race), des effets du milieu social (taille du groupe) et climatique (variation saisonnière de la durée d'éclairement) et, à un moindre degré, des effets d'interaction génotype × milieu. (© Elsevier / Inra)

porc / comportement alimentaire / comparaison de races / Piétrain / Large White

1. INTRODUCTION

The establishment of electronic single-space feed dispensers has made it possible to explore the individual feed intake pattern of large numbers of growing-finishing pigs housed in groups. First results dealing with this new kind of feeding device were published in 1992–1993 [6, 18, 27]. Detailed information was reported by De Haer and De Vries [5] and Labroue et al. [20–22] on the comparative feeding behaviour of pigs from two breeds, Large White and Landrace, which are close to each other in daily feed consumption, growth rate and lean percentage. The Piétrain breed exhibits lower average daily gain and higher carcass lean weight than the two other breeds, and has been known for a long time for its lower appetite under ad libitum feeding conditions [23, 25, 39, 40]. However, there are limited published data on the feed intake pattern of Piétrain pigs. Earlier investigations of Auffray and Marcilloux [2] and Le Cozler [24] were both conducted in the particular situation of individual penning, and involved

small numbers of Piétrain and Large White pigs.

Using the computerized feed intake recording equipment of the French central test stations ('Acema 48' feed dispensers [18, 20]), a study was carried out in one of these test stations in order to assess feed intake and feeding behaviour of Piétrain boars housed in groups, as compared to contemporary Large White boars housed in the same manner.

2. MATERIALS AND METHODS

2.1. Animals and management

Two hundred and ten Large White (LW) and 114 Piétrain (P) young boars were raised in four batches in one central test station (Beauvais, Oise, France). The numbers of herds of origin, sires and dams were 23, 68 and 120, and 13, 32 and 68 for LW and P, respectively. Piglets entered the station (post-weaning unit) at around 35 days of age and moved to the fattening unit at 65–70 days of age. Data were collected in 30 single-breed pens. The number of pigs per pen (group size) remained unchanged during the whole test period and ranged from 8 to 13 (average group size: 11.7 and 10.9 for LW and P, respectively). Each pen was equipped with an 'Acema 48' feed dispenser and a nipple drinker, and animals had 24-h access to food and water. Food was distributed in pellets and contained 9.0 MJ·kg^{-1} net energy and 170 g·kg^{-1} crude protein. Breed means for average daily gain and food conversion ratio from 35 to 95 kg liveweight and ultrasonic back-fat thickness at 95 kg liveweight are reported in *table I*.

2.2. Feed intake recording

After each visit to the feeder, the identity of the animal (via an ear-tag transponder), the feeder entry and exit times and the amount of feed consumed were registered and stored in the central monitoring equipment memory. Successive feeder visits performed by the same animal within 2 min were grouped into a single meal. This 'meal criterion' of 2 min had been established by Labroue et al. [20] using the log survivorship curve technique [4] on feed intake data from Large White and Landrace intact and castrated male pigs. Preliminary analyses showed that it is also suitable for Piétrain boars.

Primary data on feeding behaviour ('visit file') were collected over a fixed period of 12 weeks for LW and 14 weeks for P, i.e. the respective average times on test for LW and P boars. However, only part of these data were extracted and summarized for creating the working file of the present analysis. In order to study the effect of stage of growth on feed intake pattern, three 7-day periods were considered. In an attempt to equalize the average body weight of pigs from both breeds at each stage, the three weekly periods were chosen as follows: 2nd week on test for both LW and P (stage 1), 6th week for LW and 7th week for P (stage 2) and 10th week for LW and 12th week for P (stage 3). Average liveweight at stages 1, 2 and 3 were 39.6 and 38.8, 64.3 and 63.6, 89.8 and 88.6 kg for LW and P boars, respectively. In order to distinguish 'daylight' from 'nightly' feeding activity, feed intake records were calculated separately over two 12-h periods of the nycthemere: 8–20 h and 20–8 h.

The basic data set used for analysis therefore consisted of 1 944 observations per trait (324 animals × 3 stages of growth × 2 periods of day). Each of these observations was the mean value of the trait over the 7-day period of recording at each stage of growth.

Table I. Breed means for production traits.

Trait		Breed mean ± standard error	
		Piétrain (n = 114)	Large White (n = 210)
Average daily gain	(g)	719 ± 9	895 ± 6
Food conversion ratio (kg feed·kg^{-1} gain)		2.50 ± 0.02	2.39 ± 0.01
Back-fat thickness	(mm)	7.6 ± 0.2	11.2 ± 0.1

2.3. Traits

The seven following traits were calculated as weekly means on a 'half-day' basis: feed intake, number of feeder visits, number of meals, eating time (defined as the total feeder occupation time for all visits performed), time per meal (comprising both feeder occupation times and within-meal time intervals between the feeder visits), feed intake per meal and rate of feed intake (defined as the ratio of feed intake to eating time).

2.4. Statistical analysis

The experimental design had a split-plot structure with non-random repeated measurements on the same animal for any feed intake variable. Data were analysed as outlined by Gill [9] using various procedures of the SAS package [37]. Preliminary analyses showed that most of the two-way interactions involving the batch effect (e.g. batch by group size interaction) were of minor importance. These interactions were therefore deleted from the final mixed linear model of analysis, which consisted of the following terms: overall mean, fixed effect of breed (B), random effect of animal within-breed (A), fixed effects of batch (four levels), group size (two levels: 8–10 or 11–13 pigs), stage of growth (three levels: 39, 64 or 89 kg liveweight), period of day (two levels: 'daylight' or 'nightly'), fixed effects of breed by group size, breed by stage of growth, breed by period of day, stage of growth by period of day interactions, fixed effect of the three-way interaction between breed, stage of growth and period of day, and random residual error (E). The mean square for A effects (MS_A) was used for testing statistical significance of breed effects, whereas the residual mean square (MS_E) was used for testing statistical significance of other fixed main effects and interactions. However, for conditional (e.g. within stage of growth) comparisons of breeds (assessed by Student's *t*-tests), the relevant error mean square (σ^2) is a function of MS_A, MS_E and p (number of repeated measurements per individual), and the approximate numbers of degrees of freedom were determined according to Satterthwaite [38]. In addition, for the number of feeder visits and two traits expressed as ratios (feed intake per meal and rate of feed intake), preliminary examination of data had shown a substantial heterogeneity of variances across the breed stage of growth–period of day combinations as well as some positive skewness of distributions. As the relationship of standard deviations with means was approximately linear, analysis of variance for these three traits was performed on data transformed to a logarithmic scale, i.e. log (x + 1). This variance-stabilizing transformation made it possible to greatly reduce deviations from normality of the distributions. Estimates of means for the transformed variables were obtained by back transformation to the original scale. Repeatability of each feeding behaviour trait, defined as the ratio of the between-individual variance to the total phenotypic variance, was calculated from values of MS_A, MS_E, σ^2 and p, as indicated by Gill [9]. Calculations were made separately for each breed, using either 'whole-day' records, with p = three stages of growth, or 'half-day' records, with p = six stage of growth–period of day combinations.

3. RESULTS

3.1. Statistical significance of fixed effects

Results of analyses of variance are summarised for fixed main effects and interactions in *table II*. The effects of breed, stage of growth and period of day were significant for all feed intake pattern traits except those of breed and period of day for duration of meals and that of period of day for feed intake per meal. The effects of batch and group size on feed intake level were not significant, but they were significant for most other feeding behaviour traits. At least one of the two-way interactions of breed with group size, stage of growth or period of day revealed to be significant for the traits under study except eating time and rate of feed intake. Feed intake level and number of feeder visits were affected at the $P < 0.001$ level by the stage of growth × period of day interaction, whereas the breed × stage of growth × period of day interaction was significant ($P < 0.05$) only for eating time.

3.2. Average breed effects

Estimates of breed means (on a whole-day basis) are reported in *table III*. As

Table II. Significance levels for fixed effects in the analysis of variance of feeding behaviour traits.[1]

Source of variation	d.f.	Feed intake	Number of feeder visits[2]	Number of meals	Eating time	Time per meal	Feed intake per meal[2]	Rate of feed intake[2]
Batch	3	ns	*	***	***	†	***	***
Group size	1	ns	**	ns	***	**	ns	***
Breed	1	***	***	*	***	ns	*	**
Breed × group size	1	ns	ns	**	†	***	**	ns
Stage of growth	2	***	***	***	***	***	***	***
Period of day	1	***	***	***	***	ns	ns	***
Breed × stage of growth	2	***	**	*	ns	***	***	†
Breed × period of day	1	***	ns	*	ns	*	*	ns
Stage of growth x period of day	2	***	***	ns	ns	ns	ns	ns
Breed × stage of growth × period of day	2	ns	ns	ns	*	ns	ns	ns
R^2 of the model[3]		0.77	0.74	0.71	0.77	0.68	0.77	0.94

[1] ns (not significant): $P > 0.10$; † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
[2] Variables transformed to a logarithmic scale.
[3] Full model including the random effect of animal within breed.
d.f.: degrees of freedom.

Table III. Estimates of breed means and statistical significance of breed differences in feeding behaviour traits.

Trait		Breed means		
		Piétrain (n = 114)	Large White (n = 210)	Significance[1]
Feed intake per day	(kg)	1.72	2.12	***
Number of feeder visits per day		8.8	15.7	***
Number of meals per day		5.84	6.53	*
Eating time per day	(min)	49.7	55.6	***
Time per meal	(min)	9.34	9.45	ns
Feed intake per meal	(g)	300	332	*
Rate of feed intake	($g \cdot min^{-1}$)	34.8	38.1	**

[1] ns (not significant): $P > 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

expected, P boars exhibited a much lower daily feed consumption (–19 %, $P < 0.001$) than LW boars. This reduced feed intake was associated with a 10 % decrease of both eating time per day ($P < 0.001$) and rate of feed intake ($P < 0.01$). There was no breed difference in duration of meals, but P boars had meals of smaller size (–10 %, $P < 0.05$). The lower number of feeding bouts in P boars compared to LW boars was much more apparent from the number of feeder visits (8.8 vs. 15.7, $P < 0.001$) than from that of meals (5.8 vs. 6.5, $P < 0.05$).

3.3. Batch effects

There were highly significant batch effects on number and size of meals, eating time and rate of feed intake. Among the four batches, two corresponded to 'long-daylight' periods of recording (summer), one to 'short-daylight' period (winter) and the fourth to 'intermediate-daylight' period (spring). Examination of batch means showed marked effects of season on the feed intake pattern, with larger number of meals (6.8 vs. 5.9), lower feed intake per meal (291 vs. 330 g), slower rate of feed intake (34.0 vs. 37.4 $g \cdot min^{-1}$) and longer feeder occupation time (57.1 vs. 50.6 min) in the winter batch than in the two summer batches. Moreover, the proportion of feed consumed 'nightly' (from 20–8 h) was higher (33 vs. 28 %) in the summer than in the winter. Part of this season effect is probably due to that there are some daylight hours (up to 4 or 5) within the 'nightly' period (20–8 h) in the summer whereas there is essentially no daylight within the same period in the winter. It can also be mentioned that the seasonal variation in nychthemeral distribution of feed consumption was a little more pronounced in LW than in P pigs (results not shown).

3.4. Group size effects

Whatever the breed, group size did not affect feed intake level, but larger group size gave rise to fewer feeder visits per day (11.4 vs. 12.4), shorter daily feeder occupation time (50.8 vs. 54.5 min) and faster rate of feed intake (37.8 vs. 35.1 $g \cdot min^{-1}$). As regards the three meal-related traits, the effect of group size was breed-dependent. Large group size compared to small group size resulted in a larger number of meals (6.8 vs. 6.3 per day) of smaller size (326 vs. 339 g) and shorter duration (9.0 vs. 9.9 min) in LW boars, whereas it resulted in fewer

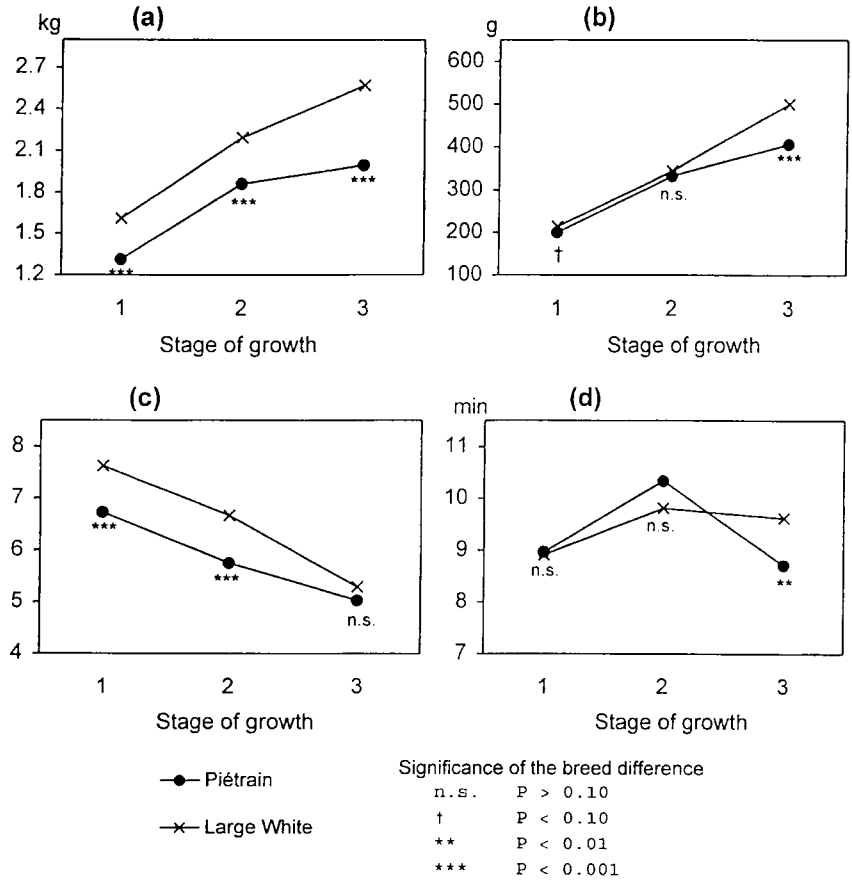

Figure 1. Estimates of average daily feed intake (a), average feed intake per meal (b), average number of meals per day (c) and average time per meal (d) by breed and stage of growth. n.s.: not significant.

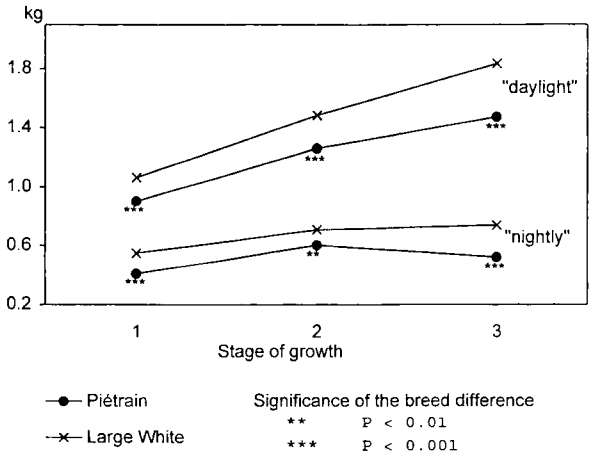

Figure 2. Estimates of average 'daylight' and 'nightly' feed intake levels by breed and stage of growth.

meals (5.7 vs. 6.0 per day) of larger size (310 vs. 291 g) and similar duration (9.4 vs. 9.3 min) in P boars. The breed difference was therefore increased for the number of meals and decreased for feed intake per meal when pigs were housed in groups of larger size. The breed by group size interaction was the strongest for time per meal, with the Piétrain boars having comparatively longer meals for large group size and shorter meals for small group size.

3.5. Stage of growth effects

The effect of stage of growth was highly significant for all feeding behaviour traits. When averaged over the two breeds, the increase in body weight of the animals was associated with higher daily feed intake (1.46, 2.03 and 2.28 kg at 39, 64 and 89 kg liveweight, respectively), smaller number of meals per day (7.2, 6.2 and 5.2), shorter eating time per day (59.3, 55.9 and 42.7 min), higher feed intake per meal (207, 338 and 451 g) and faster rate of feed intake (24.7, 36.5 and 53.4 g·min^{-1}). The number of feeder visits per day did not change between 39 and 64 kg liveweight (12.7 and 13.0, respectively), then sharply decreased (10.0 visits per day at 89 kg liveweight). Time per meal was of the same magnitude at 39 and 89 kg liveweight (8.9 and 9.2 min, respectively), but was longer in the middle of the test period (10.1 min).

However, there were significant interactions between the stage of growth and the breed effects for feed intake level ($P < 0.001$), number of feeder visits ($P < 0.01$), number of meals ($P < 0.05$), duration and size of meals ($P < 0.001$ for both traits), and marginally for rate of feed intake ($P < 0.10$). Regarding the number of feeder visits per day, the breed difference (P – LW) diminished in the course of growth while being highly significant at all stages (–8.7, –6.9 and –5.2 at stages 1, 2 and 3, respectively). As shown in *figure 1*, the breed by stage of growth interaction found for the other traits essentially reflected a marked change in the magnitude of the breed difference at stage 3 compared to both stages 1 and 2. At 39 and 64 kg liveweight, the lower feed intake level of P pigs (–0.31 kg per day, i.e. –17 %) was associated with fewer meals of similar size and duration. At 89 kg liveweight, the breed difference (P – LW) in feed intake level (–0.58 kg per day, i.e. –23 %) was larger than at the earlier stages of growth, and the lower appetite of P boars was associated with smaller size and shorter duration of a similar number of meals.

3.6. Period of day effects

There was a significant influence of period of day (8–20 h or 20–8 h) on feeding behaviour traits except for size and duration of meals, which did not differ between 'daylight' and 'nightly' meals. For the two latter traits, the interaction of period of day with breed was significant at the $P < 0.05$ level, indicating a trend to 'nightly' meals being larger and longer than 'daylight' meals in LW boars and a slightly opposite trend in P boars. The rate of feed intake was faster in the 'daylight' than in the 'nightly' period (37.0 vs. 35.8 g·min^{-1}, $P < 0.001$), and this difference was of the same magnitude in both breeds. Overall, the nychthemeral distribution of feed intake consisted of approximately 70 and 30 % consumed in the 'daylight' and 'nightly' periods, respectively. However, the effect of period of day significantly interacted ($P < 0.001$) with breed on the one hand and with stage of growth on the other hand (*figure 2*). For all stages pooled, the breed difference (P – LW) in feed intake level was –0.25 kg (i.e. –17 %) and –0.15 kg (i.e. – 23 %) in the 'daylight' and 'nightly' periods, respectively. The proportion of feed consumed between 20 and 8 h was, whatever the breed, 32.5 % at stages 1 and 2 and only 27.5 % at stage 3. This decline of the 'nightly' feeding activity at heavier body weights was also apparent from the number of feeder visits, as the pro-

portion of 'nightly' visits was close to 30 % at stages 1 and 2 and only 25 % at stage 3. The breed difference (P – LW) was greater for the number of 'daylight' meals (–0.5, $P < 0.001$) than for that of 'nightly' meals (–0.2, $P < 0.10$), but when expressing the number of 'nightly' meals as a percentage of the total number of meals per day, breed means were similar at around 30 %.

Eating time was the only variable for which the three-way interaction between breed, stage of growth and period of day was significant ($P < 0.05$) while none of the three corresponding two-way interactions reached statistical significance. As mentioned earlier, feeder occupation time was shorter for P than for LW boars. This breed effect was, however, of varying magnitude according to the stage of growth–period of day combination (*figure 3*), and it did not significantly differ from zero for 'daylight' eating time at stage 1 and 'nightly' eating time at stage 2.

3.7. Repeatabilities

Repeatability estimates for feed intake traits are presented by breed in *table IV*. Estimates obtained from analyzing 'whole-day' records refer to the average correlation among the measurements made on the same individual at different stages of growth. Repeatability was substantially lower for daily feed intake (around 0.30) than for the other feeding behaviour traits (0.50–0.60). Moreover, higher repeatability values were consistently found in LW compared to P animals, especially for feed intake, eating time per day and rate of feed intake. Estimates obtained from analyzing 'half-day' records refer to the average correlations among repeated measurements across the six stages of growth–period of day combinations. Repeatability values were similar to the preceding ones for the number of feeder visits, time per meal, feed intake per meal and rate of feed intake. This similarity suggests that the 'between-period of day' repeatability is of the same order as the 'between-stage of growth' repeatability for those traits. In contrast, repeatability estimated from 'half-day' records was lower than that estimated from 'whole-day' records for the number of meals and eating time (0.30–0.40), and was close to zero for feed intake level.

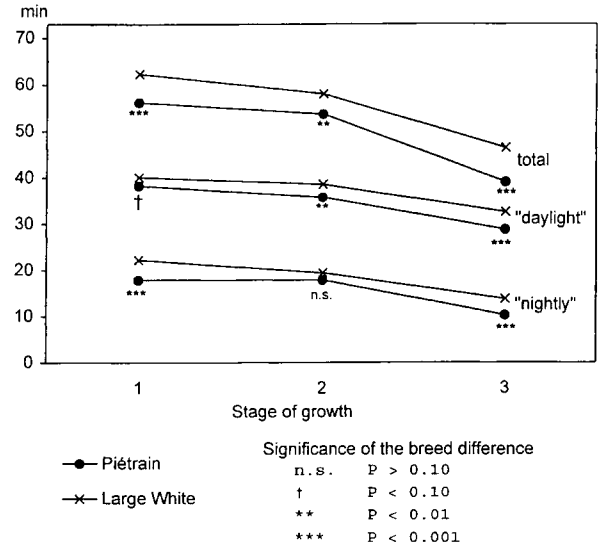

Figure 3. Estimates of average eating times (total, 'daylight' and 'nightly') by breed and stage of growth. n.s.: not significant.

Table IV. Repeatabilities of feeding behaviour traits, estimated by breed from either 'whole-day' or 'half-day' records.

Trait	Breed[1]	Repeatability	
		'Whole-day' records[2]	'Half-day' records[3]
Feed intake	P	0.25	0.07
	LW	0.38	0.04
Number of feeder visits	P	0.49	0.44
	LW	0.57	0.50
Number of meals	P	0.52	0.32
	LW	0.58	0.36
Eating time	P	0.52	0.33
	LW	0.64	0.31
Time per meal	P	0.56	0.58
	LW	0.60	0.57
Feed intake per meal	P	0.50	0.45
	LW	0.57	0.53
Rate of feed intake	P	0.55	0.58
	LW	0.78	0.80

[1] P: Piétrain; LW: Large White.
[2] Standard error of estimates: 0.025–0.061 for P, 0.023–0.044 for LW.
[3] Standard error of estimates: 0.030–0.040 for P, 0.018–0.021 for LW.

4. DISCUSSION

4.1. Effect of breed

The rate of reduction of voluntary feed intake per day in Piétrain compared to Large White boars amounted to 19 % in the present study, which falls within the range of values (13–21 %) reported in the last 40 years (e.g. [14, 39, 40]). That the rate of reduction of feed intake level in the Piétrain boars slightly increased with the animal's body weight is in agreement with the results of Martin and Buysse [25] and Lean et al. [23]. However, Sellier et al. [40] found that daily feed intake of Piétrain gilts was proportionately 0.81 that of French Landrace gilts, as well from 27 to 50 kg as from 50 to 96 kg liveweight. The decrease of daily feed intake of Piétrain compared to Large White or French Landrace boars is of the same order (16 to 19 %) in intact males, castrated males and females according to Guéblez (1993, unpublished results).

The lower daily feed consumption displayed by the Piétrain boars in this study was equally due to a shorter feeder occupation time per day and a reduced rate of feed intake (roughly –10 % for each trait in comparison with Large White boars). Moreover, this decrease of feed intake level occurred in the two periods of day considered, while being proportionately larger in the 'nightly' than in the 'daylight' period (–23 % vs. –17 %). As regards meal characteristics, the origin of the lower feed intake of the Piétrain animals appeared to be dependent on the stage of growth: it was associated either with a smaller number of meals of similar size at 39 and 64 kg liveweight or with a similar number of meals of smaller size in the later test period. It is worth noting that

Piétrain boars share with Landrace boars the feature of visiting the feed dispenser much less frequently but for a much longer time than Large White boars [5, 20, 22].

4.2. Effect of stage of growth

A curvilinear augmentation of daily feed intake occurred when the animal's body weight increased, in agreement with the classical asymptotic-type curve relating feed intake to body weight [1, 15, 17, 31]. The extent of curvilinearity was more marked for the Piétrain animals over the studied range of body weights (40–90 kg). Part of this breed difference could be ascribed to the 20–25 % smaller adult size and the 10 % lower mature feed intake (around 3.3 vs. 3.7 $kg \cdot d^{-1}$) showed by the Piétrain animals compared to the Large Whites [17].

Expressing daily feed intake on a metabolic body weight basis (weight raised at 0.60 exponent for the growing pig, according to Noblet et al. [30]) revealed that feed intake level is fairly constant across the three stages of growth while being higher in Large White (177, 180 and 173 $g \cdot d^{-1} \cdot kg^{0.60}$, respectively; average standard error [SE]: 2.8) than in Piétrain animals (146, 154 and 135 $g \cdot d^{-1} kg^{0.60}$, respectively; average SE: 3.4). Regarding the rate of feed intake expressed on a metabolic body weight basis, a substantial augmentation was brought about by the increase in body weight: from 2.8 to 3.8 $g \cdot min^{-1} \cdot kg^{0.60}$ (average SE: 0.05) in Large White boars and from 2.6 to 3.4 $g \cdot min^{-1} \cdot kg^{0.60}$ (average SE: 0.06) in Piétrain boars. This weight-dependent pattern is in contrast with earlier studies that reported a constancy or even a small decline of consumption rate per min with increasing metabolic body weight. It should, however, be noted that, in the studies reviewed by Hyun et al. [13], metabolic body weight was defined as $weight^{0.75}$. When the consumption rate data from the current study were adjusted on the latter basis, the augmentation of consumption rate with increasing metabolic body weight was markedly smoother.

Regarding the influence of stage of growth on feed intake behaviour, Piétrain and Large White animals followed the same pattern, i.e. a decrease of the daily number of feeder visits and feeder occupation time from 65 kg liveweight, a regular decline of number of meals per day, a sharp increase in rate of feed intake and size of meals, and an increasing then decreasing trend for duration of meals. These trends are in line with those described earlier for ad libitum fed pigs raised in various feeding/housing environments: individual penning [2, 3, 12], housing in groups of varying size using conventional self-feeders [11, 42], or housing in groups of 8–15 pigs using electronic single-space feed dispensers [13, 19, 41]. However, it should be mentioned that the changes in feeding behaviour during the course of growth were less marked in the 'low appetite' Piétrain animals than in the 'high appetite' Large White ones for most behavioural traits, e.g. number of feeder visits per day and feed intake per meal.

4.3. Effect of group size

In the present study, the variation in the number of animals per pen was fairly limited, i.e. 11.9 and 9.8 animals for large and small group size, respectively. The effect of group size was, however, found to be significant for the traits related to feeder occupancy (number of feeder visits and total feeder occupation time per day) as well as for the duration of meals and rate of feed intake. In agreement with Labroue et al. [19], there was a decrease of the number of feeder visits and feeder occupation time for the larger group size, whereas the rate of feed intake was increased. A much larger variation in group size (animals penned in groups of 5, 10, 15 or 20) was studied by Nielsen and Lawrence [26], and they found an effect of group size on feeding behaviour traits (especially the number of feeder visits) only at 20 pigs per pen vs. the other group sizes. In the present study, the group size

effect (small vs. large) was almost of the same magnitude as the breed effect (P vs. LW) for rate of feed intake, but the two corresponding effects for daily eating time contrasted, which resulted in a large breed difference and no group size difference for daily feed intake.

The finding that the number of pigs per pen (i.e. per electronic feed dispenser) does not influence feed intake level but brings about some change in feed intake pattern is in fairly good agreement with the results reported by Nielsen and Lawrence [27] for group size ranging from 5 to 20, and with those of Labroue et al. [19] for group size ranging from 8 to 13. The variation in the extent of group size effects could be partly related to the variation in the design of the single-space feed dispenser and consequently to the level of allowed competition for food. Comparing three feeder entrance designs offering low, medium or high protection against disturbance of the eating animal, Nielsen et al. [28] found no significant differences among them in feed intake level, number of feeder visits and feeder occupation time per day. However, using feeders with low or medium protection resulted in a faster rate of feed intake as well as in shorter time and less feed consumed per feeding bout. On the other hand, the proper effect of group size was confounded with the floor space allowance per pig in the present study and that of Labroue et al. [19] unlike the study of Nielsen and Lawrence [27] in which space allowance was held constant at 1.06 $m^2 \cdot pig^{-1}$ for all group sizes. There is evidence that space allowance and group size affect performance and feeding behaviour independently [16, 32, 33].

4.4. Effect of test batch

As found in the preceding study conducted in three French central test stations [20], batch effect was not significant for daily feed intake level but reached statistical significance for feed intake pattern traits. The present study dealt with records collected in a single station, and test batch effects can at least partly be ascribed to seasonal influences. Due to the environmental testing conditions prevailing in our study (natural-lighting regime and building controlled for ambient temperature), the seasonal influences on feed intake pattern are likely to be related more specifically to seasonal variation in length of the 'daylight' period than to seasonal variation in average temperature and/or 'daylight' vs. 'nightly' differences in temperature [29, 34, 35].

4.5. Effect of period of day

That feeding activity of pigs having 24-h access to food occurring predominantly in the 'daylight' period has been repeatedly shown under a variety of housing conditions, feeding systems and animal's body weight ranges [2, 3, 6, 8, 13, 14, 26, 43]. Even for the experiments conducted with electronic feed dispensers, comparisons between studies is, nevertheless, made rather difficult due to the broad variability of testing environments ranging from natural lighting and outdoor-like ambient temperature in an open-fronted building [43] to continuous lighting for 24 h in an environmentally regulated building [13]. Here, the overall nychthemeral distribution of feeding activity, assessed either by feed consumed or feeder occupation time, was roughly 70 and 30 % for the 'daylight' and 'nightly' periods of day, respectively. As found earlier by Auffray and Marcilloux [2] on single-penned pigs, the percentage of 'daylight' feeding activity increased in the course of the growth period (around 67.5 and 72.5 % for feed consumed and 70 and 75 % for the number of feeder visits at 39 and 89 kg liveweight, respectively). This percentage was, however, unaffected by the stage of growth when considering feeder occupation time. In contrast to Auffray and Marcilloux [2], who observed a larger size of 'daylight' meals, no effect of the period of day on time

and feed intake per meal was found. The percentage of feed consumed between 8 and 20 h also depended on the test batch (67 and 72 % in 'long-daylight' and 'short-daylight' seasons, respectively) and, to a lesser extent, on breed (68.5 and 70.5 % for Large White and Piétrain, respectively). Thus, the distribution of feeding activity during the nycthemeron appears to be influenced both by genetic factors (breed) and environmental factors (body weight, season, etc.). These effects are individually of limited magnitude (less than 5 % for the proportion of 'daylight' feed consumption), but when added together they can result in a fairly large variability of this proportion between experiments.

4.6. Repeatabilities

The prominent feature in this respect is that, whatever the breed, our repeatability estimates are noticeably lower for feed intake level than for feed intake pattern traits. This result confirms those reported by De Haer and Merks [6] and Hyun et al. [13]. In the latter study, the overall repeatability levels were similar to those found in the present study, whereas they were lower in the study of De Haer and Merks [6] when calculated within the whole period of test in group-housed animals.

The repeatability of a character for which multiple measurements can be made by temporal or spatial repetition sets an upper limit of its heritability [7]. It should be pointed out that this statement lies on the implicit assumption that the repeated measurements reflect what is genetically the same character. The results reported by Roehe et al. [36] and Von Felde et al. [41] for daily feed intake suggest that this assumption does not necessarily hold over the whole period of growth. Beyond this limitation, it is, however, worth underlining the general agreement between the situations encountered for comparative heritabilities and repeatabilities of daily feed intake versus other traits. The heritability estimates reported in the literature [5, 10, 21, 22, 41] concur to indicate that daily feed consumption has a lower heritability than the other feed intake behaviour traits (on average, 0.25–0.30 vs. 0.40–0.45).

5. CONCLUSION

The present study confirms that the feed intake behaviour of growing pigs (both level of daily feed consumption and pattern of feeding activity) is under the influence of genetic factors (here, the breed), social factors (group size), climatic factors (seasonal variation in length of daylight period), and, to some extent, genotype × environment interaction effects. The relative importance of these sources of variation is shown to be dependent on the feeding behaviour trait considered. The Piétrain breed offers a model of pig exhibiting smaller appetite, slower growth rate and increased carcass leanness. The 'between-breed' relationships found here between daily feed consumption and eating time per day or rate of feed intake are in line with what is currently known about the within-breed genetic correlations among those traits. As regards the association of daily feed consumption with meal characteristics, there is, however, some discrepancy between the results of the present breed comparison and available estimates of genetic correlations.

ACKNOWLEDGEMENTS

The authors are indebted to M. Marion, who headed the central test station in Beauvais at the time of data collection. This work was supported by a doctoral thesis scholarship given to the first author by Inra and Itp and by grants from Inra and the French Ministry of Agriculture.

REFERENCES

[1] Andersen S., Pedersen B., Growth and food intake curves for group-housed gilts and castrated male pigs, Anim. Sci. 63 (1996) 457–464.

[2] Auffray P., Marcilloux J.C., Analyse de la séquence alimentaire du porc, du sevrage à l'état adulte, Reprod. Nutr. Dev. 20 (1980) 1625–1632.

[3] Bigelow J.A., Houpt T.R., Feeding and drinking patterns in young pigs, Physiol. Behav. 43 (1988) 99–109.

[4] Clifton P.G., Analysis of feeding and drinking patterns, in: F.M. Toates, N.E. Rowland (Eds.), Feeding and Drinking, Elsevier, Amsterdam, 1987, pp. 19–36.

[5] De Haer L.C.M., De Vries A.G., Effects of genotype and sex on the feed intake pattern of group housed growing pigs, Livest. Prod. Sci. 36 (1993) 223–232.

[6] De Haer L.C.M., Merks J.W.M., Patterns of daily food intake in growing pigs, Anim. Prod. 54 (1992) 95–104.

[7] Falconer D.S., Introduction to Quantitative Genetics, 2nd edn., Longman, London, 1981.

[8] Feddes J.J.R., Young B.A., De Shazer J.A., Influence of temperature and light on feeding behaviour of pigs, Appl. Anim. Behav. Sci. 23 (1989) 215–222.

[9] Gill J.L., Repeated measurement: sensitive tests for experiments with few animals, J. Anim. Sci. 63 (1986) 943–954.

[10] Hall A.D., Hill W.G., Bampton P.R., Webb A.J., The use of feeding pattern traits in pigs as selection criteria to improve the accuracy of selection for feed conversion ratio and growth traits, in: Proceedings of the 6th World Cong. Genet. Appl. Livest. Prod., Armidale, 11–16 January 1998, vol. 23, 547–550.

[11] Hansen L.L., Hagelso A.M., Madsen A., Behavioural results and performance of bacon pigs fed "ad libitum" from one or several self-feeders, Appl. Anim. Ethol. 8 (1982) 307–333.

[12] Hsia L.C., Wood-Gush D.G.M., The temporal patterns of food intake and allelomimetic feeding of pigs of different ages, Appl. Anim. Ethol. 11 (1984) 271–282.

[13] Hyun Y., Ellis M., McKeith F.K., Wilson E.R., Feed intake pattern of group-housed growing-finishing pigs monitored using a computerized feed intake recording system, J. Anim. Sci. 75 (1997) 1443–1451.

[14] Ingram D.L., Walters D.E., Legge K.F., Variations in motor activity and in food and water intake over 24 h periods in pigs, J. Agric. Sci. Camb. 95 (1980) 371–380.

[15] Kanis E., Koops W.J., Daily gain, food intake and food efficiency in pigs during the growing period, Anim. Prod. 50 (1990) 353–364.

[16] Kornegay E.T., Notter D.R., Effects of floor space and number of pigs per pen on performance, Pig News Info. 5 (1984) 23–33.

[17] Krieter J., Kalm E., Growth, feed intake and mature size in Large White and Pietrain pigs, J. Anim. Breed. Genet. 106 (1989) 300–311.

[18] Labroue F., Guéblez R., Meunier-Salaün M.C., Sellier P., Alimentation électronique dans les stations publiques de contrôle des performances : paramètres descriptifs du comportement alimentaire, in : 25es Journées de la recherche porcine en France, Paris, 2–4 février 1993, Institut technique du porc, Paris, 1993, pp. 69–76.

[19] Labroue F., Guéblez R., Meunier-Salaün M.C., Sellier P., Effets des facteurs liés au groupe sur le comportement alimentaire des porcs en croissance, in : 26es Journées de la recherche porcine en France, Paris, 1–3 février 1994, Institut technique du porc, Paris, 1994, pp. 299–304.

[20] Labroue F., Guéblez R., Sellier P., Meunier-Salaün M.C., Feeding behaviour of group-housed Large White and Landrace pigs in French central test stations, Livest. Prod. Sci. 40 (1994) 303–312.

[21] Labroue F., Guéblez R., Sellier P., Genetic parameters of feeding behaviour and performance traits in group-housed Large White and French Landrace growing pigs, Genet. Sel. Evol. 29 (1997) 451–468.

[22] Labroue F., Maignel L., Sellier P., Noblet J., Consommation résiduelle chez le porc en croissance alimenté à volonté: méthode de calcul et variabilité génétique, in : 31es Journées de la Recherche porcine en France, Paris, 2–4 février 1999, Institut technique du porc, Paris, 1999, pp. 167–174.

[23] Lean I.J., Curran M.K., Duckworth J.E., Holmes W., Studies on Belgian Pietrain pigs, 1. A comparison of Pietrain, Landrace and Pietrain-Landrace crosses in growth, carcass characteristics and meat quality, Anim. Prod. 15 (1972) 1–9.

[24] Le Cozler Y., Production de chaleur et comportement alimentaire chez le porc en relation avec son potentiel de croissance, mémoire de DEA, Université Paris 7, 1994.

[25] Martin J., Buysse F., La capacité d'ingestion et l'influence du niveau protidique sur la croissance, la consommation et les qualités viande du porc de Piétrain, in : Colloque sur la race porcine belge Piétrain, Bruxelles, 21–22 mars 1960, Service des informations agricoles, Bruxelles, 1960, pp. 129–136.

[26] Montgomery G.W., Flux D.S., Carr J.R., Feeding patterns in pigs: the effects of amino acid deficiency, Physiol. Behav. 20 (1978) 693–698.

[27] Nielsen B.L., Lawrence A.B., The effect of group size on the behaviour and performance of growing pigs using computerised single-space feeders, Pig News Info. 14 (1993) 127N–129N.

[28] Nielsen B.L., Lawrence A.B., Whittemore C.T., Effects of single-space feeder design on feeding behaviour and performance of growing pigs, Anim. Sci. 61 (1995) 575–579.

[29] Nienaber J.A., Hahn G.L., Korthals R.L., McDonald T.P., Eating behaviour of swine as influenced by environmental temperature, in: The 4th International Symposium of A.S.A.E. on Livestock Environment, Coventry, 6–9 July 1993, pp. 937–944.

[30] Noblet J., Karege C., Dubois S., Influence of growth potential on energy requirements for maintenance in growing pigs, in: Wenk C., Boessinger M. (Eds.), Energy Metabolism of Farm Animals, EAAP Publication No. 38, ETH, Zurich, 1991, pp. 107–110.

[31] Parks J.R., A Theory of Feeding and Growth of Animals, Springer-Verlag, Berlin, 1982.

[32] Petherick J.C., Beattie A.W., Bodero D.A.V., The effect of group size on the performance of growing pigs, Anim. Prod. 49 (1989) 497–502.

[33] Randolph J.H., Cromwell G.L., Stahly T.S., Kratzer D.D., Effects of group size and space allowance on performance and behavior of swine, J. Anim. Sci. 53 (1981) 922–927.

[34] Rinaldo D., Le Dividich J., Influence de la température ambiante sur les performances de croissance du porc, Inra Prod. Anim. 4 (1991) 57–65.

[35] Rinaldo D., Salaün M.C., Le Dividich J., Influence d'une réduction de la température ambiante ou d'un abaissement nocturne de la température sur les performances du porcelet sevré, in : 21es Journées de la recherche porcine en France, Paris, 31 janvier et 1–2 février 1989, Institut technique du porc, Paris, 1989, pp. 239–244.

[36] Roehe R., Von Felde A., Looft H., Krapoth J., Kalm E., Effect of stage of growth on genetic parameters of feed intake in swine, in: Proceedings of the 5th World Cong. Genet. Appl. Livest. Prod., Guelph, 7–12 August 1994, 1994, vol. 19, pp. 185–188.

[37] SAS, SAS/Stat User's Guide, Version 6, 4th edn., vol. 2, SAS Institute Inc., Cary, NC, USA, 1990.

[38] Satterthwaite F.E., An approximate distribution of estimates of variance components, Biometrics 2 (1946) 110–114.

[39] Sellier P., Ollivier L., Résultats d'une expérience de croisement Piétrain × Large White, 1. Performance d'engraissement et d'abattage, in : 3es Journées de la recherche porcine en France, Paris, 18–19 février 1971, Institut technique du porc, Paris, 1971, pp. 19–22.

[40] Sellier P., Houix Y., Desmoulin B., Henry Y., Premières observations sur la relation entre conditions nutritionnelles et type génétique chez des porcs femelles, in : 6es Journées de la recherche porcine en France, Paris, 20–22 février 1974, Institut technique du porc, Paris, 1974, pp. 209–219.

[41] Von Felde A., Roehe R., Looft H., Kalm E., Genetic association between feed intake and feed intake behaviour at different stages of growth of group-housed boars, Livest. Prod. Sci. 47 (1996) 11–22.

[42] Walker N., The effects on performance and behaviour of number of growing pigs per monoplace feeder, Anim. Feed Sci. Technol. 35 (1991) 3–13.

[43] Young R.J., Lawrence A.B., Feeding behaviour of pigs in groups monitored by a computerized feeding system, Anim. Prod. 58 (1994) 145–152.