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Influence of environmental enrichment on the behaviour, performance and meat quality of domestic pigs

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Abstract

Three hundred and twenty pigs were reared from birth to slaughter at 21 weeks in either barren or enriched environments. The barren environments were defined as intensive housing (slatted floors and minimum recommended space allowances) and the enriched environments incorporated extra space, an area which contained peat and straw in a rack. Behavioural observations showed that environmental enrichment reduced time spent inactive and time spent involved in harmful social and aggressive behaviour while increasing the time spent in exploratory behaviour. During the finishing period (15–21 weeks) mean daily food intakes were higher and food conversion ratios were lower for pigs in enriched environments compared with their counterparts in barren environments ($P < 0.05$). Growth rates were also higher for pigs in enriched environments during this period ($P < 0.001$) and this led to heavier carcass weights ($P < 0.05$). Pigs from enriched environments also had greater levels of backfat than their counterparts from barren environments ($P < 0.001$). Environmental enrichment during rearing had a small but significant effect on meat quality. Pork from pigs reared in barren environments was less tender and had greater cooking losses than pork from pigs reared in enriched environments ($P < 0.01$). © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pigs; Environmental enrichment; Behaviour; Performance; Meat quality

1. Introduction

It is generally accepted that environmental enrichment with substrates improves the welfare of growing pigs (Wood-Gush and Beilharz, 1983; Arey, 1993). In barren rearing environments, pigs tend to redirect exploratory behaviour towards penmates

(Petersen et al., 1995), and this can lead to persistent aggression and cannibalism (Beattie et al., 1995). In addition, high levels of penmate-directed behaviour in barren rearing environments have a negative effect on the productivity of pigs due to disturbances in feeding patterns (Ruiterkamp, 1987). Morgan et al. (1998) also found lower growth rates among pigs in barren rather than enriched environments and suggested they were due to increased energy requirements for heat maintenance in the absence of substrates. Alternatively, Pearce et al. (1989) proposed that growth rates of pigs in barren environments

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were adversely affected by chronic elevations in the stress hormone cortisol.

Meat quality may also be affected by rearing environment as problems such as pale, soft and exudative (PSE) meat can be influenced by levels of preslaughter stress which, in turn, are influenced by rearing environment (Geverink, 1998). Pearce and Paterson (1993) found that pigs reared in barren environments showed greater 'reactivity' in response to stressful stimuli than those reared in enriched environments. Similarly, pigs provided with environmental enrichment during rearing showed less fearfulness towards humans than those reared in barren environments (Pearce et al., 1989). These findings suggest that providing pigs with environmental enrichment during rearing may reduce stress associated with preslaughter procedures and result in better quality pork.

Previous studies on environmental enrichment and productivity have tended to limit their use of enriching substrates to straw (Ruiterkamp, 1987; Geverink, 1998), whereas evidence suggests that earth-like materials such as peat may be more effective as enriching agents (Beattie et al., 1998). Also, environmental enrichment is often only incorporated after weaning (Warriss et al., 1983; Pearce and Paterson, 1993), whereas characteristics which can affect performance and meat quality in pigs, such as stress responsiveness, appear to be established earlier in life (Hessing et al., 1993). The objective of the present study was to assess the effects of environmental enrichment with peat, straw and extra space throughout the life of growing pigs on their behaviour, performance and meat quality.

2. Material and methods

2.1. Design

The effects of rearing in different environments (barren and enriched) were examined in a two treatment design with five replicates. Treatments were applied over a 21-week period which was divided into three stages: Stage 1, 0–7 weeks of age; Stage 2, 8–14 weeks of age and Stage 3, 15–21 weeks of age.

The number of days in each stage may have varied by ± 1 day between replicates. At the end of stage 1 and 2 there was a change in housing environment and at the end of stage 3 the pigs were slaughtered. A full description of treatments in relation to age and housing is outlined in Table 1. All animals were weighed at birth and at 7, 14 and 21 weeks of age, and behaviour was observed on a weekly basis throughout the experimental period.

2.2. Animals

Three hundred and twenty pigs were used in this study, equal numbers being allocated to the two treatments. Each replicate was composed of the litters of eight Large White \times Landrace sows which were randomly allocated to eight different boars and which farrowed in crates at approximately the same time. At 3 days post partum, four dams were selected at random and were transferred with their litters to enriched housing (pens with straw bedding with no constraints on the dams movement). The remaining four dams and their litters remained in farrowing

Table 1
Summary of number of pigs per treatment (per replicate) and housing during each stage of the experiment

Stage	Number of pigs per treatment	Housing		
		Barren	Enriched	
1	(0–4 weeks)	Four litters of 10–12 pigs	Farrowing crate	Straw bedded pen
	(4–7 weeks)	Four groups of 8 pigs	Farrowing crate	Straw bedded pen
2	(8–14 weeks)	Four groups of 8 pigs	Flat deck cage (0.36 m ² per pig)	Fully enriched pen divided into five areas (1.75 m ² per pig)
3	(15–21 weeks)	Four groups of 8 pigs	Slatted pen (0.76 m ² per pig)	Fully enriched pen divided into five areas (3.5 m ² per pig)

crates until weaning at 4 weeks of age. At weaning four boars and four gilts were chosen from each litter according to least variation from the average weight of the group. The selected boars and gilts from the four litters in enriched housing were regrouped into four groups of eight, each group consisting of one boar and one gilt from each litter. A similar procedure was performed on the pigs in barren accommodation. These groups of eight pigs remained together for the duration of the study.

2.3. Housing

2.3.1. Stage 1 (0–7 weeks)

In the first stage of life piglets were housed either in a farrowing pen (barren environment) or a straw bedded pen (enriched environment). The farrowing pen was 2.6×1.6 m and had a floor made of plastic slats. The enriched pen measured 3.6×2.2 m and had a solid floor which was bedded with unchopped straw. The dams were present for the first 4 weeks. After weaning the piglets remained in their respective environments until the end of stage 1 at 7 weeks of age.

2.3.2. Stage 2 (growing period, 8–14 weeks)

The barren environment at stage 2 consisted of flat deck cages, 2.4×1.2 m, with expanded metal floors. The enriched environment was 14 m^2 in total, divided into five areas: rooting area, straw area, sleeping area, feeding area and defecating area. The stocking density was 0.36 m^2 per pig in the barren pens and 1.75 m^2 per pig in the enriched pens.

2.3.3. Stage 3 (finishing period, 15–21 weeks)

The barren environment was a pen measuring 1.9×3.2 m with a fully slatted floor. The enriched pens were of similar design to the stage 2 enriched pens but with twice the floor area in each of the five sections. Stocking densities were 0.76 m^2 per pig in the barren pens and 3.5 m^2 per pig in the enriched pens.

A detailed description of housing at each stage is given by Beattie et al. (1995).

2.4. Husbandry

Both environments at all stages had a day/night cycle, with full lighting between 0800 and 1700 h,

and dimmed lighting for the remainder of the time. In the barren farrowing housing the environmental temperature was maintained at approximately 18°C while the average temperature of the enriched farrowing environment was 15°C . Localized supplementary heating was supplied by heat lamps over the creeps in both environments. Ambient temperature outside the sleeping kennels in stage 2 and 3 of the enriched environments ranged between 10°C and 22°C . Temperature was controlled in the barren environments at 21°C in stage 2 and 17°C in stage 3. Lactating sows were fed to appetite and from 10 days of age, creep feed was provided for the piglets in both environments. Water was available from birth for the piglets, via one water nipple, in both environments. In stages 2 and 3 in both environments feed was offered ad libitum in single space wet and dry feeders (Verba wet feeder, L. Verbakel, The Netherlands). In enriched stages 2 and 3 housing peat and straw were replenished as necessary.

2.5. Diet

Sows in both environments during lactation were offered on average 6.5 kg/day of a cereal/soya based diet supplying 14 MJ digestible energy (DE)/ kg air-dry diet. Piglets up to 7 weeks old were offered commercial creep and stage 1 feed. From 7 weeks to slaughter pigs were offered a cereal/soya based diet ad libitum. The diets offered from 8 to 14 weeks of age and from 15 to 21 weeks contained 14.2 and 13.4 MJ DE/kg and 22% and 18% crude protein, respectively. Diets at all stages were pelleted.

2.6. Behaviour

In each treatment group of eight, one boar and one gilt were chosen as focal animals. These were selected on the basis of being nearest to the average weight of the litter on the day of birth. The same focal animals were observed throughout the trial by direct observation on a weekly basis. Observations took place between 1300 and 1700 h as this part of the day has previously been identified as the most active period for growing pigs (Beattie, 1994). Observational periods for all treatments were matched in time, pen order and gender of the focal animal and were carried out by one observer. In-

dividual observational periods lasted 10 min, during which the behaviour of the focal animal and behaviour directed towards the focal animal were recorded continuously using a hand-held data recorder (Microscribe, Modµlec Technology, UK). The ethogram of behaviours which were recorded is listed in Table 2.

2.7. Performance

The weight of each animal was recorded at birth and at 7, 14 and 21 weeks of age and individual growth rates were calculated for intervening stages. Feed intakes and feed conversion ratios were calculated on a per pen basis during stages 2 and 3.

2.8. Slaughter procedures

Prior to slaughter the pigs were transported a distance of 80 km to a commercial abattoir where they spent approximately 2 h in lairage with their original penmates. The pigs were then electrically stunned and slaughtered according to normal commercial practice. Backfat was measured with an optical probe at a point 6.5 cm from the edge of the dorsal mid-line, at the level of the last rib (P_2). Carcasses were then weighed and chilled at 1°C. Meat quality measurements were carried out on all pigs. The pH of the Longissimus Dorsi muscle was measured 45 min (pH_1) and 24 h (pH_u) post mortem using an electrode probe attached to a portable pH

Table 2
Ethogram of behaviours recorded for pigs in barren and enriched environments

Behaviour	Description of behaviour
Nosing pig	Rubbing the body of a penmate with the snout or being the recipient of this behaviour. Mostly directed to the back, shoulders, belly, flank and soft tissue between the fore and hind legs
Biting pig	Nibbling, sucking or chewing ears, legs, feet or tails or being the recipient of this behaviour
Substrate explore	Sniffing, nosing or chewing straw or peat
Fixtures explore	Sniffing, touching, sucking or chewing any object which is part of the pen including bare floor
Fight	Mutual pushing parallel or perpendicular, ramming or pushing of the opponent with the head, with or without biting in rapid succession. Lifting the opponent by pushing the snout under its body
Inactive while alert	Sitting, standing or lying inactive with eyes open
Headthrusting	Ramming or pushing penmate(s) with head (each occurrence recorded separately) and being the recipient of this behaviour.
Ingestion	Feeding, drinking and eliminative behaviour
Suckling	At least half of the litter are active at the udder while the sow is in the nursing position (lying on the side with the udder fully exposed)
Manipulating sow's udder	Being active at the udder when the sow is not in the nursing posture or when less than half of the litter is present at the udder.
Locomotory	Any locomotion excluding walking e.g. running, scampering, frisking or rolling
Other	When the focal animal is not involved in any of the listed behaviours

meter (Sentron 3001 pH System, Sentron USA). All remaining meat quality assessments were carried out on cross-sectional samples of L. Dorsi muscle. These had a width of 3–4 cm and were removed 24 h postmortem from the left dorsal area of the carcass in the region of the 12th rib.

2.9. Meat quality

The method used by Koolmees et al. (1986) was used to prepare samples for determination of sarcomere length. Sarcomere lengths were calculated from a minimum of ten observations per sample according to a formula used by Cross et al. (1981). Drip loss was determined by placing a 3–4 cm slice of L. dorsi in a plastic net bag which was in turn placed inside a pre-weighed polythene bag and suspended in a chill room at 1°C for 2 days. The polythene bag plus exudate was then weighed and drip loss was calculated as a percentage of the weight of the original sample. Cooking loss was determined by placing weighed samples of L. dorsi of approximately 4 cm thickness in polythene bags and heating them in a water bath at 70°C for 50 min. The samples were then weighed and cooking loss was calculated as a percentage of the weight of the original sample. From each cooked sample ten cores, 13.5 mm in diameter and 35–40 mm long were obtained and the shear force was determined using a Warner Bratzler shear cell attached to an Instron Model 6021 Universal test machine. The shear force was determined using test speed 100 mm per minute with a 1 kN load cell calibrated to read over the range 0–20 kg.

The colour of the L. dorsi muscle was measured using a Monolight 6800 spectrophotometer (Rees Instruments, UK) using 0/45° geometry. The entire spectra were recorded from 380 to 800 nm at 1-nm intervals. CIE colour co-ordinates were calculated using 5-nm interval data using CIE (1977) data.

2.10. Statistical analysis

The data were analysed using GENSTAT, version 5 (Lawes Agricultural Trust, 1989). The behaviour of focal animals was calculated as a percentage of the observation time and behavioural data were analysed using mean values per group. Performance and meat quality parameters were also analysed using mean

values per group. An analysis of variance (ANOVA) was carried out to examine the effects of rearing environment on behaviour and performance. Meat quality parameters and backfat thickness were analysed by covariance analysis, using carcass weight as a covariate.

3. Results

3.1. Behaviour

Behavioural results are given in Table 3. Pigs in enriched environments used the substrates provided for exploratory behaviour spending more than a quarter of their time in substrate-directed behaviour. In barren environments the pigs spent more time exploring the fixtures of the pen than their enriched counterparts ($P < 0.001$). Pigs in barren environments also spent more time involved in harmful social behaviour such as nosing other pigs ($P < 0.001$ in stages 1 and 2, $P < 0.05$ in stage 3) and biting other pigs ($P < 0.001$), and aggressive behaviour such as headthrusting ($P = 0.06$ in stages 1 and 3, $P < 0.001$ in stage 2). The duration spent inactive while alert was greater in barren environments than in enriched environments ($P < 0.01$ in stage 1, $P < 0.001$ in stages 2 and 3).

3.2. Performance

Performance results are given in Table 4. Mean daily feed intakes did not differ significantly between pigs in barren and enriched environments during stage 2, however during stage 3 pigs in enriched environments had greater intakes than their counterparts in barren environments ($P < 0.05$).

There were no significant treatment effects on growth rate during stage 1 or stage 2, or on body weight at 7 and 14 weeks of age. Pigs from enriched environments had higher growth rates during stage 3 ($P < 0.001$) and were heavier than pigs from barren environments at 21 weeks of age ($P < 0.001$).

The food conversion of pigs in barren environments was better than that of those in enriched environments during stage 2 ($P < 0.05$), however during stage 3 pigs in enriched environments had better food conversion ($P < 0.05$).

Table 3
Percentage of observation time spent performing different behaviours by pigs in barren and enriched environments

Behaviour	Environment		S.E.M.	P
	Barren	Enriched		
Stage 1 (0–7 weeks)				
Substrate explore	–	31.9	–	–
Fixtures explore	21.8	2.5	0.80	< 0.001
Nosing pig	6.7	3.3	0.38	< 0.001
Biting pig	2.6	0.6	0.15	< 0.001
Headthrusting	0.4	0.3	0.05	0.06
Inactive while alert	16.5	10.4	1.15	< 0.01
Locomotory	0.3	1.3	0.15	< 0.001
Ingestion	4.4	3.1	0.56	NS
Suckling	4.7	5.4	0.65	NS
Manipulating sows udder	5.6	3.7	0.80	NS
Other	40.0	37.5	1.46	NS
Stage 2 (8–14 weeks)				
Substrate explore	–	27.8	–	–
Fixtures explore	20.7	6.9	0.90	< 0.001
Nosing pig	9.2	4.8	0.65	< 0.001
Biting pig	6.6	1.5	0.41	< 0.001
Headthrusting	0.8	0.5	0.06	< 0.001
Inactive while alert	32.2	16.6	1.46	< 0.001
Locomotory	0.1	0.2	0.04	NS
Ingestion	11.3	10.8	0.76	NS
Other	19.1	30.9	1.72	< 0.001
Stage 3 (15–21 weeks)				
Substrate explore	–	25.6	–	–
Fixtures explore	24.9	7.1	1.26	< 0.001
Nosing pig	8.3	6.1	0.69	< 0.05
Biting pig	4.3	0.9	0.25	< 0.001
Headthrusting	0.6	0.4	0.05	0.06
Inactive while alert	28.2	18.2	0.95	< 0.001
Locomotory	0.1	0.1	0.03	NS
Ingestion	15.9	15.0	1.26	NS
Other	17.7	26.6	1.83	< 0.01

The carcass characteristics of the animals from the two environments differed significantly. Pigs from enriched environments had heavier carcass weights ($P < 0.05$) and greater levels of backfat thickness than their counterparts from barren environments ($P < 0.001$).

3.3. Meat quality

Pork from pigs reared in enriched environments showed lower cooking losses and shear force values than pork from pigs reared in barren environments (cooking loss (%): B 26.88, E 25.78, S.E.M. 0.288, $P < 0.01$; Shear force (kg/cm^2): B 3.01, E 2.74,

S.E.M. 0.062, $P < 0.01$). There were no significant effects of rearing environment on the remaining meat quality parameters.

4. Discussion

The results from the present study agree with previous studies which found large differences in the behaviour of pigs reared in barren and enriched environments (Beattie, 1994; Petersen et al., 1995). When given access to substrates, the focal animals spent more than a quarter of their time exploring them. In the absence of these substrates they spent

Table 4
Average performance of pigs from barren and enriched rearing environments

Parameter	Environment		S.E.M.	P
	Barren	Enriched		
Stage 1 (0–7 weeks)				
Birth weight (kg)	1.6	1.7	0.02	NS
Growth rate (kg/day)	0.32	0.32	0.005	NS
7 week weight (kg)	16.9	17.1	0.25	NS
Stage 2 (8–14 weeks)				
Feed intake (kg/day)	1.36	1.41	0.022	NS
Food conversion	1.69	1.82	0.033	< 0.05
Growth rate (kg/day)	0.81	0.78	0.013	NS
14 week weight (kg)	57.1	55.5	0.646	NS
Stage 3 (15–21 weeks)				
Feed intake (kg/day)	2.23	2.38	0.050	< 0.05
Food conversion	2.82	2.58	0.075	< 0.05
Growth rate (kg/day)	0.80	0.93	0.014	< 0.001
21 week weight (kg)	95.0	100.2	0.953	< 0.001
Carcase weight (kg)	73.9	77.8	0.91	< 0.05
Backfat (mm)	11.9	15.1	0.57	< 0.001

more time exploring their pen and penmates. The persistent nosing and chewing of penmates is thought to reflect redirected rooting behaviour in pigs (Van Putten and Dammers, 1976) and in the present study the time spent performing this type of behaviour was significantly greater in barren than enriched environments. The reduction in aggressive behaviour in enriched environments agrees with previous work (Schaefer et al., 1990; Blackshaw et al., 1997) and may reflect a reduced need to retaliate against persistent manipulation by penmates (Beattie et al., 1995). Similarly, the increased time spent inactive while alert in barren environments may reflect a greater need for vigilance against penmates (Schouten, 1986).

The higher average ambient temperature in barren environments may also have affected the behaviour of the pigs in the resident pen. This is supported by earlier work which found relationships between increased ambient temperature and increased time spent inactive by pigs (Pearce and Paterson, 1993; Hicks et al., 1998). However high ambient temperatures have also been associated with reduced aggression in pigs (Hicks et al., 1998), which suggests that, in the present study, physical surroundings had a greater influence on this type of behaviour than ambient temperature. The smaller space allowance in

barren environments may also have influenced behaviour as there is evidence that reducing space allowance leads to an increase in aggressive (Ewbank and Bryant, 1972; Kelley et al., 1980) and harmful social behaviour in pigs (Randolph et al., 1981). In the present study it was impossible to differentiate between the relative effects of enrichment and space allowance on behaviour, however an earlier study by Beattie et al. (1996) found that space allowance had little influence on behaviour compared with environmental enrichment.

Earlier studies on the influence of environmental enrichment on productive performance in pigs have yielded conflicting results. Schaefer et al. (1990) and Horrell (1992) found that enriching the environment of pigs improved their growth rate, whereas Pearce and Paterson (1993) and Blackshaw et al. (1997) found no improvement in productivity when pigs were provided with environmental enrichment. In the present study, pigs in enriched environments had higher growth rates at finishing which were due to higher feed intakes and better food conversion. Pigs from enriched environments also had backfat which was on average 3.2 mm thicker than their counterparts in barren environments. As the pigs in both environments were of similar genetic stock, it is possible that the higher intakes in enriched environ-

ments resulted in these pigs reaching their maximum potential for lean deposition and therefore depositing more fat than pigs in barren environments (Clutter and Brascamp, 1998).

Ruiterkamp (1987) associated high levels of penmate-directed behaviour with reduced feed intake in growing pigs. In the present study, it is possible that higher levels of harmful social and aggressive behaviour around the feeder in barren pens led to lower feed intakes during the finishing period. This type of behaviour may also have led to higher levels of stress in barren environments which have been shown to adversely affect food conversion efficiency (Barnett et al., 1983). The fact that lower growth rates were shown in barren environments during the finishing period and not during the growing period agrees with previous work (Beattie et al., 1995) and may reflect a cumulative effect of penmate-directed behaviour on performance. The performance of pigs in barren environments may also have been adversely affected by the higher ambient temperatures (Morrow-Tesch et al., 1994) and smaller space allowances (Kornegay and Notter, 1984). Previous research suggests that space allowance may have a greater impact on the performance of finishing pigs rather than younger pigs due to their changing behavioural requirements (Pearce and Paterson, 1993).

Pigs from enriched environments produced pork which had a lower shear force and which showed less cooking loss than their counterparts from barren environments. These differences in quality did not appear to be attributable to differences in preslaughter stress as pH values were similar across both treatments. Furthermore, the increased shear force of pork from barren pigs cannot be accounted for by any muscle shortening as sarcomere lengths did not differ between treatments. A possible explanation for the treatment differences is that enriched pigs had higher levels of intramuscular fat which have previously been associated with improved tenderness and water holding capacity in pork (Candek-Potokar et al., 1998). This is supported by the finding that pigs from enriched environments had significantly greater levels of backfat which generally results in higher levels of intramuscular fat (Barton-Gade, 1987). Other factors such as proteolytic enzymes (Blanchard et al., 1998) or collagen maturity (Warkup and

Kempster, 1991) which may be related to faster growth rates may have led to the improvements in meat quality in enriched environments.

Although the parameters affected by environmental enrichment in the present study, namely tenderness and cooking loss, are of commercial importance, the magnitude by which they were improved may not be commercially significant. However, this study demonstrated a link between rearing environment and meat quality through improved production performance.

5. Conclusion

This study agrees with previous similar studies in showing that environmental enrichment improves the welfare of pigs by reducing anti-social behaviour. Performance was also enhanced by enrichment in the finishing period and this was possibly associated with a reduction in aggressive and harmful social behaviour. Pigs in enriched environments also showed an improvement in meat quality which appeared to be related to the improved performance. Therefore an indirect link can be drawn between reduced levels of anti-social behaviour in enriched environments and improved meat quality.

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References

- Arey, D.S., 1993. The effect of bedding on the behaviour and welfare of pigs. *Anim. Welf.* 2, 235–246.
- Barnett, J.L., Hemsworth, P.H., Hand, A.M., 1983. Effects of chronic stress on some blood parameters in the pig. *Appl. Anim. Ethol.* 9, 273–277.
- Barton-Gade, P.A., 1987. Meat and fat quality in boars, castrates and gilts. *Livest. Prod. Sci.* 16, 187–196.
- Beattie, V.E. 1994. The Effects of Environmental Enrichment on the Domestic Pig. Ph.D. Thesis, The Queen's University of Belfast, Northern Ireland.

- Beattie, V.E., Walker, N., Sneddon, I.A., 1995. Effects of environmental enrichment on behaviour and productivity of growing pigs. *Anim. Welf.* 4, 207–220.
- Beattie, V.E., Walker, N., Sneddon, I.A., 1996. An investigation of the effect of environmental enrichment and space allowance on the behaviour and production of growing pigs. *Appl. Anim. Behav. Sci.* 48, 151–158.
- Beattie, V.E., Walker, N., Sneddon, I.A., 1998. Preference testing of substrates by growing pigs. *Anim. Welf.* 7, 27–34.
- Blackshaw, J.K., Thomas, F.J., Lee, J.-A., 1997. The effect of a fixed or free toy on the growth rate and aggressive behaviour of weaned pigs and the influence of hierarchy on initial investigation of the toys. *Appl. Anim. Behav. Sci.* 53, 203–212.
- Blanchard, P.J., Mantle, D., Chadwick, J.P., Willis, M., 1998. Effect of feeding a high energy/low protein diet to finishing pigs on growth and meat quality. In: *Proc. Br. Soc. Anim. Sci., Annual Meeting, Scarborough*, p. 34.
- Candek-Potokar, M., Zlender, B., Bonneau, M., 1998. Effects of breed and slaughter weight on longissimus muscle biochemical traits and sensory quality in pigs. *Ann. Zootech.* 47, 3–16.
- CIE, 1977. Colorimetry. CIE Publication No. 15, Official Recommendations of the Commission Internationale de L'Eclairage.
- Clutter, A.C., Brascamp, E.W., 1998. Genetics of performance traits. In: Rothschild, M.F., Ruvinsky, A. (Eds.), *The Genetics of the Pig*, CAB International, pp. 427–462.
- Cross, H.R., West, R.L., Dutson, T.R., 1981. Comparison of methods for measuring sarcomere length in beef semitendinosus muscle. *Meat Sci.* 5, 261–266.
- Ewbank, R., Bryant, M.J., 1972. Aggressive behaviour amongst groups of domesticated pigs kept at various stocking rates. *Anim. Behav.* 20, 21–28.
- Geverink, N.A., 1998. *Preslaughter Treatment of Pigs: consequences for welfare and meat quality*. Ph.D. Thesis, Wageningen Agricultural University, The Netherlands.
- Hessing, M.J.C., Hagelsø, A.M., Van Beek, J.A.M., Wiepkema, P.R., Schouten, W.G.P., Krukow, R., 1993. Individual behavioural characteristics in pigs. *Appl. Anim. Behav. Sci.* 37, 285–295.
- Hicks, T.A., McGlone, J.J., Whisnant, C.S., Kattesh, H.G., Norman, R.L., 1998. Behavioral, endocrine, immune, and performance measures for pigs exposed to acute stress. *J. Anim. Sci.* 76, 474–483.
- Horrell, I., 1992. Effects of environmental enrichment on growing pigs (abstract). *Anim. Prod.* 54, 483.
- Kelley, K.W., McGlone, J.J., Gaskins, C.T., 1980. Porcine aggression: measurement and effects of crowding and fasting. *J. Anim. Sci.* 50, 336–341.
- Koolmees, P.A., Korteknie, F., Smulders, F.J.M., 1986. Accuracy and utility of sarcomere length assessment by laser diffraction. *Food Microstruct.* 5, 71–76.
- Kornegay, E.T., Notter, D.R., 1984. Effects of floor space and number of pigs per pen on performance. *Pig News Info.* 5 (1), 23–33.
- Lawes Agricultural Trust, 1989. *Genstat 5 Reference Manual*, Clarendon Press, Oxford.
- Morgan, C.A., Deans, L.A., Lawrence, A.B., Nielsen, B.L., 1998. The effects of straw bedding on the feeding and social behaviour of growing pigs fed by means of single-space feeders. *Appl. Anim. Behav. Sci.* 58, 23–33.
- Morrow-Tesch, J.L., McGlone, J.J., Salak-Johnson, J.L., 1994. Heat and social stress effects on pig immune measures. *J. Anim. Sci.* 72, 2599–2609.
- Pearce, G.P., Paterson, A.M., 1993. The effect of space restriction and provision of toys during rearing on the behaviour, productivity and physiology of male pigs. *Appl. Anim. Behav. Sci.* 36, 11–28.
- Pearce, G.P., Paterson, A.M., Pearce, A.N., 1989. The influence of pleasant and unpleasant handling and the provision of toys on the growth and behaviour of male pigs. *Appl. Anim. Behav. Sci.* 23, 27–37.
- Petersen, V., Simonsen, H.B., Lawson, L.G., 1995. The effect of environmental stimulation on the development of behaviour in pigs. *Appl. Anim. Behav. Sci.* 45, 215–224.
- Randolph, J.H., Cromwell, G.L., Stahly, T.S., Kratzer, D.D., 1981. Effects of group size and space allowance on performance and behaviour of swine. *J. Anim. Sci.* 53, 922–927.
- Ruiterkamp, W.A., 1987. The behaviour of grower pigs in relation to housing systems. *Neth. J. Agric. Sci.* 35, 67–70.
- Schaefer, A.L., Salomons, M.O., Tong, A.K.W., Sather, A.P., Lepage, P., 1990. The effect of environment enrichment on aggression in newly weaned pigs. *Appl. Anim. Behav. Sci.* 27, 41–52.
- Schouten, W.G.P., 1986. *Rearing Conditions and Behaviour in Pigs*. Ph.D. Thesis, University of Wageningen, The Netherlands.
- Van Putten, G., Dammers, J., 1976. A comparative study of the well-being of piglets reared conventionally and in cages. *Appl. Anim. Ethol.* 2, 339–356.
- Warkup, C.C., Kempster, A.J., 1991. A possible explanation of the variation in tenderness and juiciness of pig meat (abstract). *Anim. Prod.* 52, 559.
- Warriss, P.D., Kestin, S.C., Robinson, J.M., 1983. A note on the influence of rearing environment on meat quality in pigs. *Meat Sci.* 9, 271–279.
- Wood-Gush, D.G.M., Beilharz, R.G., 1983. The enrichment of a bare environment for animals in confined conditions. *Appl. Anim. Ethol.* 10, 209–217.