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Original article

Influence of age at nutritional restriction on growth and sexual development of gilts

A Prunier

INRA, Station de Recherches Porcines, 35590 Saint-Gilles, France

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Summary — Large White females were fed on a plane of nutrition close to *ad libitum* during the entire experimental period (CTRL group, n = 48) or restricted during a limited period of their growth (RP1 group: 28–62 kg, RP2 group: 64–96 kg, RP3 group: 97–131 kg, n = 48/group). Blood samples were taken before 200 and 230 days of age in order to detect cyclic gilts by assaying their progesterone levels. Animals were slaughtered at ≈ 260 d of age and their genital tracts were examined. Overall feed intake, feed conversion ratio and daily gain were significantly lower in restricted than in CTRL gilts (average daily gain: 678, 680, 668 and 741 g/day respectively in RP1, RP2, RP3 and CTRL groups, $P < 0.05$). At slaughter, animals from the 3 restricted groups had similar live weights but were lighter (152 *vs* 164 kg live weight, $P < 0.05$) and leaner than CTRL (fat thickness: 29.5, 30.5, 28.0 and 34.1 mm respectively, in RP1, RP2, RP3 and CTRL groups). Respectively, 9, 43 and 76% of the gilts were puberal at 200, 230 and 260 days of age. The percentage of cyclic females was not influenced by treatment at 200 and 260 days of age while it was higher in CTRL (50%) and RP1 (56%) groups than in RP2 (35%) and RP3 (29%) groups at 230 days of age ($P < 0.05$). At 260 days of age, ovarian and genital tract weights were not influenced by treatment either in prepuberal or in cyclic gilts. The number of corpora lutea in cyclic females was also similar in the 4 treatment groups. This experiment confirms that feed restriction can delay the attainment of puberty and shows that its effect depends on the time of application.

gilt / puberty / nutritional restriction / growth / progesterone

Résumé — Influence du moment d'application d'une restriction alimentaire sur la croissance et le développement sexuel des truies. *Des femelles de race Large White étaient nourries selon un plan d'alimentation proche du niveau* ad libitum *pendant toute la durée de l'expérience (groupe CTRL,* n *= 48) ou rationnées de près de 30% pendant une période limitée de leur croissance (groupe RP1: 28–62 kg, groupe RP2 : 64–96 kg, groupe RP3 : 97–131 kg,* n *= 48/groupe). Des prises de sang étaient effectuées juste avant 200 et 230 j d'âge afin de détecter les femelles cycliques par dosage de la progestérone. Toutes les femelles étaient abattues aux alentours de 260 j d'âge et les tractus génitaux étaient prélevés et disséqués. Sur l'ensemble de l'expérience, la consommation d'aliment, l'indice de consommation et le gain de poids quotidien étaient plus faibles chez les femelles rationnées que chez celles du groupe témoin (gain moyen quotidien: 678, 680, 668 et 741 g/j respectivement pour les groupes RP1, RP2, RP3 et CTRL;* P *< 0,05). À l'abattage, les animaux des 3 groupes restreints avaient un poids vif similaire mais ils étaient plus légers (152* vs *164 kg,* P *< 0,05) et plus maigres que les témoins (épaisseur de lard: 29,5; 30,5; 28,0 et 34,1 mm respectivement pour les groupes RP1, RP2, RP3 et CTRL;* P *< 0,05). Respectivement 9, 43 et 76%*

des femelles étaient pubères à 200, 230 et 260 j d'âge. Ce pourcentage de truies cycliques était indépendant du traitement à 200 et 260 j d'âge alors qu'à 230 j, il était plus élevé dans les groupes CTRL (50%) et RP1 (56%) que dans les groupes RP2 (35%) et RP3 (29%), (P < *0,05). À 260 j d'âge, le poids des ovaires et du tractus génital était indépendant du traitement chez les femelles prépubères et cycliques. Le nombre de corps jaunes des femelles cycliques était également indépendant du traitement. Cette expérience confirme qu'une restriction alimentaire peut induire un retard de puberté et montre que l'effet produit dépend du moment auquel elle intervient.*

truie / puberté / rationnement alimentaire / croissance / progestérone

INTRODUCTION

Nutrition during the rearing period and the consequent alterations of the live weight and body composition may influence the sexual development of the gilt (Etienne *et al,* 1983; Den Hartog and Noordewier, 1984; Kirkwood and Aherne, 1985; Prunier *et al,* 1987). However, it is not clear whether the influence of feed restriction is a direct effect on the attainment of puberty or is mediated by its effects on live weight and/or body composition. On the one hand, most experiments with moderate feed restriction show alterations in live weight and body composition without concomitant modification of age at puberty (Aherne *et al,* 1976; Etienne *et al,* 1983; Den Hartog and Noordewier, 1984). On the other, some authors have shown negative relationships between average daily gain or backfat thickness before puberty and age at puberty (Den Hartog and Noordewier, 1984; King, 1989). Since sexual maturation of the gilt occurs in 4 phases (Camous *et al,* 1985): a perinatal phase, an infancy period (2nd month of age), a phase of initiation of sexual development (3rd to 5th months of age) and a waiting period (6th month of age to puberty), undernutrition during one or many of these periods may have specific effects. This point has been poorly investigated. Piglets whose milk intake was reduced during the first 8 weeks of life are slightly lighter at 140 days of age than non-restricted piglets (5.4 kg live weight difference) but reach puberty at the same age (Nelson and Robison, 1976) while undernutrition between 28 and 61 kg live weight delays age at first œstrus (Etienne *et al,* 1983). The aim of the present study was to determine if undernutrition during one of the periods of sexual development has specific effects on the attainment of puberty.

MATERIALS AND METHODS

Animals

Sixty-four Large White gilts from 20 groups of 3 or 4 littermates were allocated to 4 treatment groups on a within-litter basis. Three replicates of this design were carried out with females born in November and December 1986, June 1987 and February 1988. Age and live weight at allotment were respectively 77 ± 5 days and 28 ± 3 kg (mean ± SD).

All the animals received the same diet containing 12.9 MJ of digestible energy per kg, 17.3% of protein and 0.83% of lysine. Up to slaughter, the control females (CTRL) were fed according to a scale close to *ad libitum* and ranging between 1.1 kg/day at 20 to 25 kg live weight and 3.2 kg/day from 105 kg of live weight until slaughter. Restricted gilts received the same diet as the CTRL females until they were offered 70% of the CTRL diet during a limited period occurring between 28 and 62 kg live weight (period P1) for the RP1 group, 64 and 96 kg (period P2) for the RP2 group and, 97 and 131 kg (period P3) for the RP3 group. For the RP2 and RP3 groups, food supply was progressively reduced on 5 days. After the period of restriction, restricted gilts were pair-fed with the CTRL ones. Moments of feed restriction were based on live weight in order to be sure that restricted animals would attain the same live weight at the end of the last period of restriction. All the females were weighed at weekly intervals and on the day of slaughter. They were housed in groups of 4 under natural daylight. Feed refusals were collected daily, pooled and measured weekly and feed intake was then calculated at weekly intervals.

Two blood samples were collected by venipuncture at a 9–13 day interval before 200 days of age and 2 others before 230 days. Plasma progesterone was assayed on these samples according to the method described by Terqui and Thimonier (1974). When at least 1 of the 2 samples collected before 200 days of age contained > 2 ng progesterone/ml, the female was considered cyclic and prepuberal otherwise. The same method was applied at 230 days of age.

Females of the same litter were slaughtered the same day at 261 ± 2 days of age. The genital tracts were removed and trimmed of their ligaments. The weights of the ovaries and of the genital tract (uterine horns plus cervix plus vagina) were recorded. Ovaries were dissected, the presence of corpora lutea was depicted and their number was determined.

Backfat thickness was measured at slaughter in 3 sites (on the mid line at the level of the gluteus medius muscle, 8 cm laterally at the level of the 3rd–4th lumbar vertebrae and 6 cm laterally at the level of the 3rd–4th ribs) with a Fat-O-Meat'er device as described by Desmoulin *et al* (1984). The mean of the 3 sites was calculated for statistical analysis.

Statistical analysis

Since animals were penned in groups, means of feed intake and feed conversion ratio were calculated for each pen and submitted to statistical analysis. The effects of the treatments on the percentage of cyclic females at 200, 230 and 260 days of age were assessed with the χ^2 test. The other data were analyzed by analysis of variance using the GLM procedure of the Statistical Analysis Systems Institute (1985). The model for growth performance included replicate and treatment as main effects, the litter within replicate effect and the interaction between replicate and treatment. Characteristics of the genital tracts were analyzed separately for prepuberal and cyclic gilts. The model included replicate, treatment and the interaction between these effects.

RESULTS

Feed intake and growth performance

Age of the females at the end of each period of feed restriction is given in table I. Live weight at slaughter was similar in the 3 restricted groups but significantly lower than in the CTRL group.

During the period of restriction, feed intake compared to the CTRL group was reduced between 28.3 and 31.9% and average daily gain was decreased between 33.1–34.2% (table II). During this period, the ratio of feed conversion in the restricted group was non-significantly increased. Thereafter, growth rate and ratio of feed conversion were always improved in the restricted groups even though the difference with the CTRL group was seldom significant (table II). Feed restriction induced an overall significant decrease of 12.5 to 14.0% for feed intake ($P < 0.05$), and 8.2 to 9.8% for growth rate ($P < 0.05$). Ratio of feed conversion was improved between 3.7 and 6.3% in the 3 restricted groups but this effect was significant only in the RP1 and RP2 groups.

Finally, feed restriction resulted in lower backfat thickness at slaughter (table II). This effect was more pronounced in the group with the latest period of restriction.

Sexual development

Respectively, 9, 43 and 76% of the gilts were puberal at 200, 230 and 260 days of age. Treatment had no effect on the attainment of puberty at 200 and 260 days of age while the percentage of cyclic gilts was significantly lower in the RP2 and RP3 groups than in the CTRL and RP1 groups at 230 days of age (fig 1).

Weights of the ovaries and of the genital tract were significantly lower in prepuberal (ovaries: 7.1 ± 0.2 g, genital tract: 268 ± 20 g, mean ± standard error of the mean, n = 45) than in cyclic gilts (ovaries: 13.6 ± 0,4 g, genital tract: 757 ± 15 g, n = 145, $P < 0.01$). However, within prepuberal and cyclic groups of females they did not differ between treatments. Similarly, the number of corpora lutea (16.1 ± 0.2) in cyclic females was not influenced by the feed restriction.

Table I. Influence of treatments on age at the end of the 3 periods of feed restriction and live weight at slaughter (mean ± SEM).

	Treatment			
	CTRL	*RP1*	*RP2*	*RP3*
Age (days)				
End of P1	125 ± 1^a	149 ± 1^b	127 ± 1^a	127 ± 1^a
End of P2	168 ± 1^a	187 ± 1^b	186 ± 1^b	168 ± 1^a
End of P3	213 ± 1^a	230 ± 1^b	232 ± 1^b	232 ± 1^b
Live weight (kg)				
Slaughter	164 ± 2^a	153 ± 2^b	153 ± 2^b	151 ± 2^b

a,b Means with different superscripts in the same line differ significantly ($P < 0.05$).

DISCUSSION

Undernutrition during a limited period of growth without the possibility of compensate for it thereafter induced an overall reduction of live weight and fat tissue development at a fixed age and an improvement of feed efficiency. The effect on fat tissue was more pronounced when feed restriction occurred later in development while the effect on feed efficiency was higher when feed restriction occurred earlier. The influence of the time of restriction on fat tissue development was expected since the rate of fat deposition increases during growth (Metz *et al*, 1980; Den Hartog and Noordewier, 1984). The effect

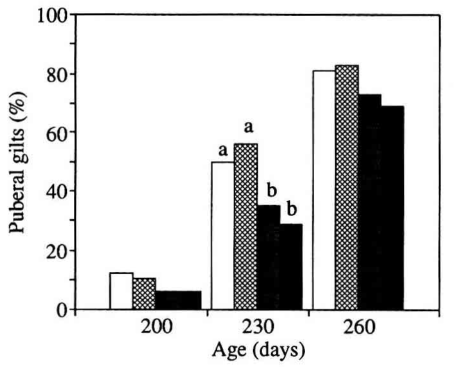

Fig 1. Effects of treatment on the attainment of puberty in gilts (CTRL, RP1, RP3 and RP4). At 230 days of age, percentages with different superscripts differ significantly ($P < 0.05$).

Table II. Influence of treatments on feed intake, growth performance, feed conversion ratio and back-fat thickness (mean ± SEM).

Treatment	*CTRL*	*RP1*	*RP2*	*RP3*	*Overall statistical significance*
Feed intake (kg/day)					
During P1	2.01 ± 0.05^{a}	1.41 ± 0.02^{b}	2.05 ± 0.05^{a}	2.04 ± 0.02^{a}	***
During P2	2.88 ± 0.04^{a}	2.82 ± 0.01^{a}	1.96 ± 0.03^{b}	2.86 ± 0.01^{a}	***
During P3	3.15 ± 0.01^{ab}	3.17 ± 0.01^{a}	3.12 ± 0.01^{a}	2.26 ± 0.01^{c}	***
During P4	3.20 ± 0.06	3.20 ± 0.12	3.12 ± 0.09	3.18 ± 0.15	NS
Daily gain (kg/day)					
During P1	717 ± 12^{a}	477 ± 10^{b}	724 ± 15^{a}	715 ± 9^{a}	***
During P2	836 ± 15^{b}	901 ± 13^{a}	550 ± 13^{c}	727 ± 13^{b}	***
During P3	785 ± 15^{a}	834 ± 15^{a}	808 ± 14^{a}	525 ± 14^{b}	***
During P4	646 ± 19	659 ± 24	655 ± 19	679 ± 22	NS
Feed conversion ratio (feed intake/daily gain)					
During P1	2.81 ± 0.03	2.96 ± 0.06	2.84 ± 0.06	2.85 ± 0.03	NS
During P2	3.46 ± 0.04^{a}	3.13 ± 0.04^{b}	3.57 ± 0.08^{a}	3.46 ± 0.05^{a}	***
During P3	4.05 ± 0.03^{ab}	3.82 ± 0.09^{b}	3.85 ± 0.08^{b}	4.32 ± 0.08^{a}	***
During P4	4.94 ± 0.09^{a}	4.80 ± 0.20^{a}	4.73 ± 0.19^{ab}	4.34 ± 0.19^{b}	*
Fat depth (mm)					
	34.1 ± 0.8^{a}	29.5 ± 0.6^{bc}	30.5 ± 0.6^{b}	28.0 ± 0.6^{c}	***

NS $P > 0.1$, *$P < 0.05$, *** $P < 0.01$. [a,b,c] Means with different superscripts in the same line differ significantly ($P < 0.05$).

of the time of undernutrition on feed efficiency can also be explained. During the period of restriction, feed efficiency was non-significantly reduced. This result is in agreement with those of Agde *et al* (1978) and Kirchgessner *et al* (1979) showing that, when feed intake is limited to 70% or less of the *ad libitum* intake, feed efficiency decreases, the fraction of energy devoted to growth being reduced. After the period of restriction, growth rate and feed efficiency were improved. This observation of compensatory growth is in agreement with Adge *et al* (1978) and Kirchgessner *et al* (1979). Thus, it seems normal that the overall influence of restriction on feed efficiency, measured on animals at the same age but with different live weight at the end-point depends on the time at which it is imposed and that it is all the more positive since it occurs earlier in growth.

In our study, puberty was delayed when undernutrition occurred during the waiting phase, while there was no effect when it occurred earlier during the period of sexual initiation. Applying the feed restriction at the beginning (RP2) or at the end of the waiting phase (RP3) gave the same result.

Aherne *et al* (1976), Friend *et al* (1981) and King (1989) also observed a retardation in puberty when feed restriction was imposed during the last 2 months preceding puberty with feed intake varying between 60 and 80% of the *ad libitum* level. Contrary to our results, Etienne *et al* (1983) showed that puberty is delayed when feed restriction is applied between 28 and 61 kg live weight. However, differences between the 2 studies can explain this discrepancy :

– feed restriction was applied until 149 days of age for our RP1 gilts instead of 169 days in the experiment of Etienne *et al* (1983);

– undernutrition was less severe in our experiment than in the previous one (feed intake: 1.41 *vs* 1.27 kg/days, average daily gain: 477 *vs* 393 g/day).

Our results suggest that a direct effect of undernutrition on sexual development exists, since the percentage of cyclic gilts at 230 days of age depended on the time of feed restriction while live weight was not modified and variations in fat thickness did not follow the same pattern. This influence of undernutrition can be explained by alterations in the secretion of neuropeptides and/or of various hormones which is known to be influenced by nutrient supply (insulin, growth hormone, cortisol, thyroxine). These endocrine alterations are likely to modify gonadotropin secretion by the pituitary or to act directly on follicular development at the ovarian level (Britt *et al*, 1988; Booth, 1990).

This experiment confirms that feed restriction can delay the attainment of puberty and shows that this effect depends on the time of application of the feed restriction: the last phase of the sexual development of the gilt (waiting phase) seems more sensitive. Moreover, it provides evidence that nutritional modulation of the reproductive function can occur independently of changes in body weight or composition. The endocrine bases of this phenomenon need further investigation.

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