

Mechanisms mediating the stimulatory effects of the boar on gilt reproduction

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The major stimulatory effects of boar presence on female pig reproduction are well documented. The boar can stimulate the early appearance of first oestrus in the prepubertal gilt, the lactating sow and the weaned sow. Additionally, boar presence may influence the exhibition and detection of oestrus, together with the sow's receptivity (see Hemsworth & Barnett, 1990). Boar involvement in other aspects of sow reproduction such as the maintenance of cyclicity and pregnancy have also been postulated, although few research data are currently available. In this review the prepubertal gilt is used as the model for response of female pigs to boar stimuli, as most of the research data is to be found in this area.

Since the major boar effects have been known for some time it may appear surprising that the mechanism controlling them is not well understood. This may be partly due to the variation observed between studies in female response to boar contact, probably reflecting confounding factors such as genotype, climatic and housing environment, nutritional status and the age of the gilt. There is also evidence that the manner of boar exposure will influence the response of the female, since variations in the length and frequency of the exposure period and, possibly, the size of the exposure pen all affect the level of stimulation perceived by the female.

These interactions clearly influence the response of gilts to boar exposure. They therefore receive early attention in this review. The roles of individual components of the boar in gilt stimulation are then considered. Finally endocrine responses of gilts to boar exposure, or exposure to boar-component stimuli, are evaluated and a tentative mechanism of action of the boar effect is postulated.

Non-boar factors influencing the efficacy of the boar effect

The data presented in Table 1 demonstrate that the pubertal response of the gilt to boar contact does not occur in a fixed-time period, even when the age of the gilt at the start of boar exposure is held constant. In most cases this is thought to be due to non-boar factors influencing the ability of the gilt to respond to boar stimulation. It is therefore pertinent to review these factors briefly in relation to boar-induced puberty in the gilt.

Genotype

Genetic influences on the natural attainment of puberty have been discussed in several recent reviews (Hughes, 1982; Christenson, 1986; Dyck, 1988). The relationship between genotype and boar-induced puberty attainment in gilts is, however, less well defined.

Between-breed differences in pubertal response to boar contact have been reported by several authors. While the extent of boar usage in these trials was variable, the consensus would be that Landrace gilts reach boar-induced sexual maturity earlier than do those of other breeds but that little difference is apparent amongst these other breeds (see Clark *et al.*, 1970; Christenson & Ford, 1979; Hutchens *et al.*, 1982; Allrich *et al.*, 1985). The same authors have also reported that heterosis

Table 1. Variation in age at puberty in gilts exposed to mature boars

Reference	Herd	Average gilt age at start of boar contact (days)	Days of puberty	Age at puberty (days)
Eastham <i>et al.</i> (1984)	Nottingham, UK	160	7.4	166.9
Brooks & Cole (1970)	Nottingham, UK	165	7.4	172.4
Pearce (1982)	Nottingham, UK	167	8.4	175.0
Eastham <i>et al.</i> (1986b)	Nottingham, UK	160	11.3	177.3
Kirkwood & Hughes (1979)	Leeds, UK	167	12.0	179.0
Paterson <i>et al.</i> (1989a)	Medina, Australia	165	12.7	177.0
Paterson & Lindsay (1981)	Medina, Australia	160	15.5	177.0
Kirkwood & Hughes (1981)	Leeds, UK	160	18.8	182.0
Killian <i>et al.</i> (1987)	Missouri, USA	155	20.8	191.5
Pearce & Hughes (1987b)	Leeds, UK	165	34.2	198.0
Kirkwood <i>et al.</i> (1981)	Leeds, UK	160	47.6	207.6
Booth (1984b)	Cambridge, UK	160	50.0	210.0
Paterson <i>et al.</i> (1989a)	Muresk, Australia	165	71.7	236.8

is shown in the ability of gilts to respond to boar stimulation, although the actual reduction in pubertal age as a result of cross-breeding is not great.

Paterson *et al.* (1989a) observed large differences in gilt age at puberty in response to boar contact in two herds in which the selection policies were widely different. In the herd in which selection was based on growth performance mean pubertal age of gilts in response to daily boar contact from 165 days of age was 178 days. On the other hand, in Herd 2, for which the selection policy was based on litter size, gilts had a mean age at puberty in response to the same boar exposure regimen of 237 days. While some confounding factors relating to the climatic environment provided by these two herds were present, these results do suggest a possible influence of long-term selection policy on the ability of gilts to respond to boar stimulation. While this may reflect differences in gilt growth rate, and hence liveweight, at the start of boar exposure it may also indicate a negative genetic correlation between age at first farrowing and litter size (see Vangen, 1986).

Nutrition

The review of Aherne & Kirkwood (1985) concluded that, while severe undernutrition of the young gilt could result in delayed puberty attainment, there was little evidence to support an inhibitory effect of mild dietary restriction on sexual maturation. Nevertheless, there is evidence to indicate that the gilt needs to attain threshold levels of liveweight before she is able to respond to puberty stimulation. For example, the study of King (1989) indicated that age at puberty increased linearly as liveweight of the gilt at boar introduction (170 days of age) was reduced. Furthermore, this result appears to be due to liveweight, rather than body fat content, since in a second experiment King (1989) reported that gilts with higher levels of body fat (at a given body weight) at 165 days of age tended to be later reaching puberty than their leaner counterparts.

Thus, any experimental protocol that includes either severe restriction of feed intake before puberty or boar contact from a very early age is likely to result in demonstrable nutritional influences on the ability of the gilt to respond to boar stimulation. The latter point is well illustrated by the study of Burnett *et al.* (1988), who reported that liveweight and backfat level exerted a decreasing influence on the ability of the gilt to respond to boar contact as gilt age at the start of this contact increased. Such results suggest that a higher proportion of gilts in the older age groups at first boar exposure are likely to have attained the necessary thresholds for liveweight and backfat, and hence are capable of responding to boar stimulation.

Climatic environment

Many studies in the USA have compared gilt response to boar contact under 'confined' or 'non-confined' conditions (Christenson, 1981; Rampacek *et al.*, 1981; Caton *et al.*, 1986a). The results of these studies suggest that confinement may delay puberty attainment in gilts by approximately 4–7 days.

Gilts housed in confined conditions may be less subject to seasonal temperature (and, possibly, photoperiod) fluctuations than are their non-confined contemporaries. Table 2 provides typical data relating season of boar exposure to puberty attainment in gilts, and indicates that the gilt tends to be more responsive to boar stimulation in the winter months. Furthermore, although the limited data that are available tend to be contradictory it appears likely that any seasonal effects that are operative exert a similar effect on both boar-induced and natural puberty attainment in gilts. However, exposure to boars partly overrides the depressive effects of season on gilt puberty (Table 3). Booth & Baldwin (1983) reported that sows became acyclic over the summer after the removal of their olfactory bulbs. This observation, together with our work, would suggest that seasonal depressions in reproductive activity in female pigs may be overcome by providing olfactory stimulation from boars.

Table 2. The effects of season of boar exposure on puberty attainment in gilts

Reference	Gilt age at start of boar contact (days)	Gilt age at puberty (days)	
		Autumn/winter	Spring/summer
Mavrogenis & Robison (1976)	140	199.3	198.8
Rampacek <i>et al.</i> (1981)	150	221.9	236.5
Christenson (1981)*	146	(81.3%)	(75.2%)
Cronin <i>et al.</i> (1983)†	203	(91.4%)	(91.2%)
Paterson <i>et al.</i> (1989a)			
Herd 1	165	174.5	179.9
Herd 2	165	220.5	252.5
Paterson <i>et al.</i> (1989b)	175	186.4	203.9

*Percentage of gilts cyclic by 9 months of age.

†Percentage of gilts cyclic by 35 weeks of age. (This study involved 2484 gilts, and the data for individual seasons relating to the percentage of gilts cycling by 35 weeks of age were 90.2, 92.1, 93.7 and 88.8 for autumn, winter, spring and summer respectively.)

Table 3. Seasonal influences on puberty attainment in boar-exposed and non-boar-exposed gilts

Season at start of boar exposure	Proportion of gilts attaining puberty within 60 days*			
	No boar contact		Daily boar contact	
	Study 1	Study 2	Study 1	Study 2
Spring	0.71 (5/7)	0.40 (25/63)	1.00 (8/8)	0.84 (54/64)
Summer	0 (0/8)	0.16 (5/31)	0.88 (7/8)	0.72 (23/32)
Autumn	0.44 (4/9)	0.40 (19/47)	0.88 (7/8)	0.87 (39/45)
Winter	—	0.46 (6/13)	—	0.93 (14/15)

*Study 1 (Paterson *et al.*, 1989b): cut-off age was 235 days.

Study 2 (A. M. Paterson & G. P. Pearce, unpublished data): cut-off age was 225 days.

Data relating the individual effects of photoperiod and temperature to the efficacy of the boar effect are limited. However, a study by Diekman & Hoagland (1983) does suggest that photoperiod may influence gilt response to boar contact during periods of decreasing, but not increasing, natural daylength (Table 4).

Table 4. The effects of supplementary light on puberty attainment in boar-exposed and control gilts (no. in parentheses) (from Diekman & Hoagland, 1983)

Treatment	Mean age at puberty of responding gilts (days)	
	Increasing daylength	Decreasing daylength
Control (no supplementary light)	200 (13)	199 ^{ab} (16)
Control + supplementary light	213 (15)	197 ^{ab} (15)
Boar exposure (no supplementary light)	192 (14)	205 ^a (15)
Boar exposure + supplementary light	187 (13)	185 ^b (16)

Means in the same column with different superscripts differ ($P < 0.01$).

The influence of ambient temperature on the gilt's ability to respond to boar stimulation is yet to be defined. To date all that can be stated is that extrapolation from studies such as that of Pearce & Hughes (1985) tentatively suggests that high ambient temperatures may reduce the efficacy of the boar effect.

Housing

The relationships between housing and reproduction are dealt with in detail by Hemsworth & Barnett (1990). It is, however, relevant to discuss the major interaction that housing conditions will have with boar-induced puberty attainment in gilts.

The effects of transport and other 'management stressors' (e.g. mixing and relocation) on boar-induced puberty in gilts have been adequately reviewed by Hughes (1982). Other housing variables are usually placed in the two categories of group size (number of gilts/pen) and stocking density. In these areas few research data are available to relate their effects to boar-induced puberty of gilts.

Data on the relationship between group size and the efficacy of the boar effect are extremely limited. Most studies confound the effects of group size and space allowance in relation to the boar effect (e.g. Mavrogenis & Robison, 1976; Christenson & Ford, 1979; Cronin *et al.*, 1983; Hemsworth *et al.*, 1986). Indeed, the only study that defines the roles of space allowance, group size and boar contact is that of Christenson (1984). The results of this work suggest that rearing gilts in groups of 3 reduced the proportion of gilts cycling by 9 months of age relative to those females housed in groups of 9, 17 or 27 per pen (proportions being 0.57, 0.78, 0.80 and 0.81 respectively). A reduction in 'stimulatory interactions' between gilts is suggested as the cause of this reduced response in small groups of gilts (Christenson, 1984).

The study of Ford & Teague (1978) reversed the conditions of the Christenson (1984) experiment by holding group size constant but varying the space allowance given to each gilt. Their results suggest that reducing the space allowance/gilt by 25 or 50% had little effect on the efficacy of

the boar effect. However, it should be noted that the actual space allowances allocated were relatively low (0.93, 0.70 and 0.47 m²/pig).

Causes of variation in the efficacy of the boar effect

The preceding discussion has briefly outlined some of the major genetic and environmental factors that may influence the efficacy of the boar effect. Variations in these factors, both between and within studies, certainly explain some of the inconsistency seen in gilt response to boar stimulation. The other causes of this variation in gilt response relate to the manner of boar exposure. In particular, the influences of the individual boar, the degree of contact allowed between boar and gilts, and the frequency and duration of boar contact must be considered.

Between-boar variations

A clear effect of boar age on the efficacy of boar-induced precocious puberty in gilts has been demonstrated by Kirkwood & Hughes (1981). These authors suggested that boars may not be able to stimulate puberty attainment in the gilt until they reach an age of approximately 9–10 months. Zimmerman & Kopf (1986) indicate that the 9-month-old boar may be as stimulatory as older boars and hence that boars are likely to achieve their full stimulatory ability at an age between 6.5 and 9 months.

Once boars have reached a sufficient age to exert full stimulating effect it is possible that between-boar variations may still exist in ability to induce precocious puberty in gilts. Such variations, should they exist, are likely to be related to either the level of pheromone release of the boar or his libido (see below). Unfortunately, no studies have yet been conducted to elucidate possible between-boar variations in stimulus effect. Casual observation suggests that the boar's libido level has little influence on his ability to induce early puberty attainment in gilts. Equally, while the known boar pheromones have been shown to increase in concentration with boar age (Booth, 1975), group rearing (Bonneau & Desmoulin, 1980; Narendran *et al.*, 1980) and copulation (Andresen, 1977; Claus, 1977), little is known concerning the relative stimulus value of mature boars (9 months of age and older) with different concentrations of pheromones in their blood or saliva. Of interest in this context is the study of Booth (1987) who compared the stimulating ability of Large White and Göttingen miniature boars, since the Göttingen boar is known to have concentrations of salivary pheromones 10- to 20-fold greater than those found in domestic boars (Booth, 1984a). The results of this study indicate that, despite its small stature, the Göttingen miniature boar is at least as stimulatory for puberty attainment in gilts as is the domestic boar (proportion of gilts responding to no boar exposure, or exposure to a Large White or a Göttingen miniature boar being 0, 0.5 and 0.75 respectively).

Effects of full compared with restricted boar contact

Early studies on the boar effect tended not to differentiate between full boar contact and the use of restricted or fence-line contact. More recent experiments have shown that fence-line contact is, in fact, far less effective as a puberty stimulation technique than is full physical contact with the boar (see Table 5). The common commercial practice of housing selected gilts in a pen adjacent to one or more mature boars is therefore unlikely to provide adequate puberty stimulation unless full physical contact with the mature boar is allowed on a daily basis (see below).

Length of the daily exposure period to the boar

In the review of Hughes (1982) the limited data available indicated that little or no difference in gilt pubertal response was apparent when boar contact was allowed on either a continuous or a

Table 5. The effects of full and limited boar contact on puberty attainment in gilts

Reference	Experimental period	Degree of boar contact	No. of gilts	Proportion reaching puberty	Mean pubertal age of responding gilts (days)
Karl bom (1981/2)	142 days -2nd oestrus	None	19	—	198
		Continuous fence line	17	—	183
		Continuous fence line + full boar contact for 20 min/day	17	—	163
Deligeorgis <i>et al.</i> (1984)	156-210 days	None	21	0.19	191
		Fence line for 20 h/day	21	0.38	192
		Full for 20 h/day	21	0.76	168
Caton <i>et al.</i> (1986b)	180-210 days	Continuous fence line	20	0.10	199
		Full contact for 30 min/day	19	0.53	198

Table 6. The effects of continuous and once-daily boar contact on puberty attainment in gilts

Reference	Duration of boar contact (days)	No. of gilts/treatment	Proportion responding			Mean days to puberty		
			30 min/day	Continuous	Control	30 min/day	Continuous	Control
Kirkwood & Hughes (1980a)	165-250	10	—	—	—	34	30	67
Van Lunen & Aherne (1987)	140-150	24	0.68	0.65	0.29	70	55	72
Hemsworth <i>et al.</i> (1988)*	176-216	16	0.93	0.81	0.31	13	19	30

*The once-daily boar contact in this experiment was for 5 min only.

Table 7. The effects of length of daily boar exposure on the efficacy of the boar effect in gilts

Reference	Length of daily boar exposure period (min)	No. of gilts	Age of gilts (days)	Average days to puberty	Proportion responding
Caton <i>et al.</i> (1986b)	5	20	180-210	16.5	0.40
	15	20	180-210	13.1	0.35
	30	19	180-210	20.2	0.53
Paterson <i>et al.</i> (1989b)	2	13	160-240	24.9	1.00
	10	14	160-240	7.4	0.71
	30	13	160-240	11.7	0.92

30 min/day basis. The subsequent studies of Van Lunen & Aherne (1987) and Hemsworth *et al.* (1988) support this conclusion (see Table 6), suggesting that the necessary boar stimuli can be perceived by the gilt in a relatively short period of time. How little daily boar contact is actually necessary has been the subject of several recent studies. The results of this work (Table 7) suggest that a daily boar exposure period of 5-10 min/day may be adequate for gilt stimulation.

As discussed later the boar effect is considered to be due to a synergism between boar pheromones and the tactile/behavioural interactions associated with exposure to the boar. It might therefore be expected that giving gilts boar contact for either a limited time each day or under conditions

that allow avoidance of the boar (e.g. large exposure pen or a large group of gilts) may reduce the efficacy of the effect. In fact, in the only study conducted in this area little effect of either group size during boar exposure or the size of the test pen was seen when boar contact was allowed for 5 or 20 min/day (P. E. Hughes, unpublished data; Table 8). Interestingly, the results of this study indicate that 5 min/day of boar contact may be inadequate and hence that the above conclusion that 5–10 min/day is sufficient to maximize the boar effect is probably an underestimation.

Table 8. The effects of group size and test arena area on the efficacy of the boar effect (P. E. Hughes, unpublished data)

	20 min/day boar contact*			5 min/day boar contact*		
	No. of gilts	Days to puberty	Proportion responding	No. of gilts	Days to puberty	Proportion responding
Test group size						
8 gilts	16	12.9	0.87	16	24.1	0.87
4 gilts	16	15.3	0.87	16	21.7	0.75
2 gilts	16	14.0	0.80	16	25.6	0.87
Test arena size						
Large	24	13.7	0.86	24	23.5	0.79
Small	24	14.3	0.83	24	24.2	0.87

*Boar contact began at 160 days of age and continued for 40 days.

Frequency of boar contact

Studies in mice (Drickamer, 1987) have indicated that the efficacy of male-stimulated puberty in the female is more dependent on the regular reinforcement of stimuli from the male than the total time that the female is exposed to the male. This suggests that regular male exposure is a prerequisite for maximum stimulation of puberty in females.

Recent studies in Australia (Paterson *et al.*, 1989a, b) were designed to test this hypothesis in the pig. The first of these experiments considered the efficacy of giving gilts boar contact for 0, 1 or 10 days and compared these with a group of gilts given daily boar contact until puberty attainment. The results (Table 9) show that, while limited boar exposure does affect puberty attainment, gilts require the repeated stimulation provided by daily boar contact to maximize the boar effect. In a further study (Paterson *et al.*, 1989b) puberty attainment was compared in groups of gilts receiving boar contact for 0, 2, 5 or 7 days/week from 175 to 235 days of age. This experiment was conducted in 3 replicates at different times of the year and hence treatment results are to some extent confounded by season. However, the data (Table 10) do suggest that daily boar contact is necessary for maximum puberty stimulation in the young gilt.

Number of boars used

Many studies on the boar effect have used groups of boars to provide the necessary stimuli for gilt puberty. Unfortunately, little information has been provided on the relative efficacy of single boars and groups of boars. In an early report, Brooks & Cole (1970) found that a weekly rotation of pairs of boars was more stimulatory to gilt puberty than was exposure to a single boar. However, these observations must be treated with caution as the gilts in the rotation group were not only exposed to a rotation of boars but also received daily contact with 2 boars and had additional fence-line contact with a further boar. More recently Kirkwood (1980) has reported little difference in the efficacy of the boar effect when applied using either a single boar or two boars on alternate days. The only other published data in this area are those of Van Lunen & Aherne (1987) who

Table 9. The effects of number of days of boar contact on puberty attainment in the gilt (from Paterson *et al.*, 1989a)

No. of days of boar contact*	Herd 1			Herd 2		
	No. of gilts	Average days to puberty	Proportion responding†	No. of gilts	Average days to puberty	Proportion responding†
0	17	51.4	0.65	14	105.8	0.43
1	17	41.5	0.76	15	95.4	0.47
10	16	28.5	0.81	15	84.7	0.67
Daily	15	12.7	1.00	14	71.7	0.86

*Starting at a gilt age of 165 days.

†Gilts reaching puberty by 245 days of age (Herd 1) or 300 days of age (Herd 2).

Table 10. The influence of frequency of boar contact on the efficacy of the boar affect (from Paterson *et al.*, 1989b)

	Frequency of boar exposure (days/week)			
	0	2	5	7
January				
Mean intervals to puberty (days)	—	36.4	34.3	28.7
Proportion reaching puberty	0/8	7/8	7/8	7/8
May				
Mean intervals to puberty (days)	48.0 ^a	32.6 ^b	33.8 ^b	11.4 ^c
Proportion reaching puberty	4/9	8/9	8/8	7/8
October				
Mean intervals to puberty (days)	44.6 ^a	32.3 ^b	18.4 ^c	16.5 ^c
Proportion reaching puberty	5/7	7/8	8/8	8/8

Means with different superscripts are significantly different: a-b and b-c, $P < 0.05$; a-c, $P < 0.01$.

indicated that the use of groups of boars may even reduce the stimulatory value of the boar effect when compared with the efficacy of single boar exposure. These authors suggested that the interactions occurring between boars in the multiple-boar exposure treatment may have frightened the gilts, resulting in boar avoidance or, at least, less frequent interactions between boars and gilts.

Effects of early boar contact

Most research studies have used the daily introduction of a mature boar to young gilts once they reach 150–170 days of age. However, this initial contact with a boar may not be novel to the gilts since they are likely to be reared in contact with castrated or entire male contemporaries. Such a rearing regimen has been suggested to be inhibitory to sexual maturation in response to mature boar contact, possibly because gilts become habituated to boar-originating stimuli (Brooks & Cole, 1969).

Experiments conducted at the University of Nottingham and elsewhere have documented that housing the young gilt in all female or mixed sex (with castrates or entire male contemporaries) groups has little or no influence on the pubertal response of the gilt to contact with a mature boar from 160 days of age (Paterson & Lindsay, 1980; Cole *et al.*, 1982). Furthermore, housing gilts from

70 to 160 days of age in fence-line contact with a mature boar has little or no effect on the response of gilts to subsequent full boar exposure at 160 days of age (Eastham *et al.*, 1986a), even when the same boar is used throughout (Eastham & Cole, 1987).

However, all the above experiments utilized relocation of gilts at 160 days of age in addition to the start of exposure to a mature boar at this time. Eastham & Cole (1987) allowed fence-line contact for gilts with a mature boar from 70 to 160 days of age and then relocated the gilts or left them in their original accommodation. Subsequently, the gilts received daily full boar contact with a different mature boar. The results of this study clearly demonstrated that, under these conditions, relocation was an important component of the boar effect, since relocated gilts reached puberty significantly earlier than did their non-relocated counterparts (Table 11). This suggests that the 'stress' of relocation is required for the full boar effect to be shown when contact with a mature boar does not constitute a novel experience.

Table 11. Puberty attainment in gilts reared in fence-line contact with a mature boar and subsequently given exposure to a novel mature boar either alone or in conjunction with relocation at 160 days of age (from Eastham & Cole, 1987)

	Novel boar only	Novel boar + relocation	Significance
No. of gilts	31	32	
Proportion of gilts reaching puberty by 210–213 days of age	0.39	0.78	$P < 0.001$
Mean interval from start of treatment to puberty (days)	89.3	20.2	$P < 0.001$

Components of the boar effect

To understand how the boar effect works it is necessary to elucidate those components of boar exposure that have a stimulatory value in terms of accelerated gilt maturation. The boar himself may be seen as constituting four possible stimulatory components, these being visual, auditory, tactile and olfactory cues. In addition, the actual process of taking gilts to a boar for stimulation must be considered since this is usually involved in the application of the boar effect.

Daily movement

The studies of Kirkwood & Hughes (1980b) and Pearce & Hughes (1985) suggest that a daily pen change is slightly stimulatory for gilt puberty relative to control animals, but that the degree of stimulation is considerably less than that afforded by a pen change plus boar exposure (Table 12). It is therefore not surprising that the pubertal response of the gilt to boar contact tends to be better when exposure occurs in the boar's pen rather than the home pen of the gilts (Table 13). Furthermore, it was suggested by Kirkwood & Hughes (1980b) that conducting the boar exposure test in the boar pen would not only provide the gilts with the stimulus of daily movement but would also allow exposure to an accumulation of boar pheromones within that pen. However, the more recent study of Pearce & Hughes (1985) did not show any advantage of exposing gilts in the boar pen over exposure in a 'new' pen cleaned daily.

Table 12. The relative effects of daily pen change and boar exposure on puberty attainment in gilts

Reference	Control		Daily pen change*		Daily pen change + boar exposure*	
	Days to puberty	Proportion responding	Days to puberty	Proportion responding	Days to puberty	Proportion responding
Kirkwood & Hughes (1980b)	50†	0.70 (7/10)	46†	1.00 (10/10)	33†	0.80 (8/10)
Pearce & Hughes (1985)	80‡	0.36 (4/11)	76‡	0.42 (5/12)	45‡	0.80 (8/10)

*Treatments began at a mean gilt age of 165 days.

†Mean.

‡Median.

Table 13. The stimulus value of the boar effect for trials conducted in the pen of the gilt or the boar

Reference	No. of gilts/treatment	Proportion of gilts responding*		
		Control	Boar taken to gilts	Gilts taken to boar
Scheimann <i>et al.</i> (1976)	16-25	0.31	0.46	0.78
Van Lunen & Aherne (1987)	24	0.29	0.48	0.68

*Response was measured for 17 days, from a mean gilt weight of 85 kg, by Scheimann *et al.* (1976) and for 130 days, from a gilt age of 140 days, by Van Lunen & Aherne (1987).

Visual cues

It is difficult to reproduce exactly the visual appearance of a boar without providing some of the other boar-originating cues such as auditory and tactile stimulation. In view of this the studies that have been performed have used either castrated or long-term androgenized castrated males. The mature castrated male is likely to be similar to a mature boar in appearance, although it will, of course, lack testes and exhibit some differences in tissue distribution in the body. On the other hand the androgenized castrate should more closely resemble the appearance of the intact male, but is also likely to exhibit 'normal' entire-male behaviour (tactile cues) and, possibly, emit 'normal' auditory cues (Booth, 1980).

In an early study by Kinsey *et al.* (1976) it was suggested that contact for prepubertal gilts with a castrated male provided as effective a stimulation to puberty as exposure to an intact boar. This would indicate that the visual component of the boar was of primary importance in the boar effect. However, Pearce & Hughes (1987b) clearly demonstrated that visual cues presented by a castrated male without other exogenous boar stimuli were considerably less effective in stimulating gilt puberty than were the full range of boar-originating cues offered by an entire boar (see Table 14).

Auditory cues

Few definitive data are available on the role of auditory cues in the boar effect. Once again the study of Kinsey *et al.* (1976) indicates that the provision of auditory cues (recorded boar chants in isolation) is equivalent to contact with a mature boar for puberty stimulation in the gilt. In contrast, Pearce & Hughes (1987b) suggest that auditory stimuli are, at most, a minor part of the boar effect (Table 14). Indeed, these latter studies failed to find a significant change in either the proportion of gilts responding to stimulation or gilt age at puberty when a recording of boar chants was added to exposure to a long-term androgenized castrate male.

Table 14. The effect of boar visual, auditory and olfactory stimuli on puberty attainment in gilts (adapted from Pearce & Hughes, 1987b)

Boar component stimuli provided	Experiment 1		Experiment 2	
	Median days to puberty	Proportion responding*	Median days to puberty	Proportion responding*
Visual + tactile	68.0 ^{ac}	0.76 (13/17)	—	—
Visual + tactile + auditory	67.5 ^a	0.56 (10/18)	66.0 ^a	0.58 (7/12)
Visual + tactile + auditory + androstenes	58.5 ^a	0.78 (14/18)	—	—
Visual + tactile + auditory + urine	—	—	49.0	0.75 (9/12)
Visual + tactile + auditory + androstenes + urine	—	—	39.0	0.78 (7/9)
Entire boar	35.5 ^{bd}	0.89 (16/18)	33.0 ^b	1.00 (11/11)

*By 240 days of age.

Within columns a vs b means are significantly different ($P < 0.05$); c vs d means are significantly different ($P < 0.01$).

Tactile cues

It is difficult to define what is meant by tactile cues in the context of the boar effect. Essentially, it is a term used to describe any physical interaction between boar and gilts, and may therefore refer to both casual contact and full courtship behaviour. It is not possible to provide such tactile cues in isolation since they must be associated with an active boar, i.e. visual, and possibly auditory and olfactory stimuli will also be provided. The androgenized castrate male certainly provides both visual and tactile cues (see Pearce & Hughes, 1987b), but appears to be relatively ineffective in stimulating early puberty attainment in the gilt (Table 14).

Conversely, when prepubertal gilts are given access to visual, auditory and olfactory stimuli from the boar but are denied full physical contact (i.e. fence-line contact is used) little puberty stimulation is evident (Table 5). It therefore appears that boar-originating tactile cues are not, on their own, major stimulants for gilt puberty, but that entire boars are also of low stimulus value if they are denied the opportunity to utilize tactile stimulation. This suggests that tactile cues act either additively or synergistically with other boar-originating cues. Indeed, since the long-term androgenized castrate, when used with a recording of boar chants, is unable to significantly advance puberty attainment this strongly suggests that tactile cues from the boar act in concert with olfactory stimuli.

Olfactory cues

The preceding discussion indicates that neither daily movement nor visual, auditory and tactile stimuli from the boar is the primary component of the boar effect. Thus, by elimination we must conclude that the boar produces an olfactory stimulus (primer pheromone) that will alter the endocrine status of the prepubertal gilt. This conclusion was verified by the study of Kirkwood *et al.* (1981) when gilts from which the olfactory bulbs had been excised were shown to be unresponsive to boar stimulation.

This raises the question as to the identity of the pheromones involved. The two known boar pheromones (5 α -androstene and 3 α -androstene) are principally found in the urine and saliva of boars, and are recognized to have signalling pheromone properties (Reed *et al.*, 1974). Kirkwood *et al.* (1983) and Booth (1984b) reported that neither of these pheromones was very effective on their own or in combination for stimulating gilt puberty (Table 15). However, there was an indication in the studies of Kirkwood *et al.* (1983) that 3 α -androstene may have some role in the boar effect.

The major site of release of this pheromone is in the frothy saliva secreted by the submaxillary salivary glands of the boar in response to sexual arousal (Booth, 1980; Perry *et al.*, 1980). Since the serous cells of these glands undergo hypertrophy at a boar age between approximately 8 and 10 months (i.e. it is at this time that they begin to accumulate appreciable amounts of 3 α -androsteno), a role for this pheromone in the boar effect would explain the inability of young boars to stimulate early puberty in gilts (see above).

To study submaxillary salivary gland pheromone involvement in the boar effect, Pearce *et al.* (1988) compared the ability of boars to stimulate gilt puberty after the removal of these glands. Their results indicate that the sialectomized boar is significantly less effective in stimulating gilt puberty than is the unoperated boar, but that a boar lacking only the submaxillary salivary gland pheromones still has some stimulatory effect on the prepubertal gilt (median intervals to puberty for control, sialectomized boar and unoperated boar exposure groups were 64, 39 and 16 days respectively). This may indicate that the non-olfactory stimuli provided by the boar do initiate a degree of sexual development in the gilt, but that this is considerably less than that afforded by an intact boar releasing salivary pheromones. Alternatively, pheromones released from sites other than the submaxillary salivary glands (e.g. urine) may be involved in the boar effect (see Table 14).

Table 15. The effects of isolated boar pheromones on puberty attainment in the gilt

	Proportion of gilts reaching puberty*		
	Kirkwood <i>et al.</i> (1983)		
	Trial 1	Trial 2	Booth (1984b)
Control	0.25 (2/8)	—	0.17 (1/6)
5 α -Androstenone	0.25 (2/8)	0.12 (1/8)	—
3 α -Androstenol	0.50 (4/8)	0.38 (3/8)	—
5 α -Androstenone + 3 α -androstenol	0.38 (3/8)	0.25 (2/8)	—
5 α -Androstenone + 3 α -androstenol + saliva	—	—	0.33 (2/6)
Boar exposure	—	1.00 (7/7)	1.00 (6/6)

*By 220 days of age (Kirkwood *et al.*, 1983—trial 1), 210 days of age (Kirkwood *et al.*, 1983—trial 2), or 240–247 days (Booth, 1984b).

At this stage it is clear that neither boar-originating pheromones in isolation nor contact with non-pheromone producing boars is an effective stimulus to gilt puberty. This implies that boar pheromones act synergistically with the boars' non-olfactory stimuli to elicit the full boar effect. To study this relationship Pearce & Hughes (1987b) provided the two known pheromones on carrier animals (long-term androgenized castrated boars). In addition, since the carrier animals would also provide the visual and tactile cues of the boar, the experiment was conducted in the presence or absence of exogenous boar-originating auditory stimulation. The results of these studies (Table 14) suggested that the provision of the visual, auditory, tactile and known olfactory boar-originating stimuli was sufficient to mimic the puberty-stimulating effect of an entire boar in those gilts that perceived the stimuli. Failure to perceive the boar-originating stimuli by some gilts may have been due, in part, to the provision of the boar pheromones in the absence of their binding protein (pheromaxein: Booth & White, 1988), although the use of boar saliva in association with 3 α -androsteno and 5 α -androsteno (but in the absence of a carrier animal) has not proved to be an effective puberty stimulant in the gilt (Booth, 1984b).

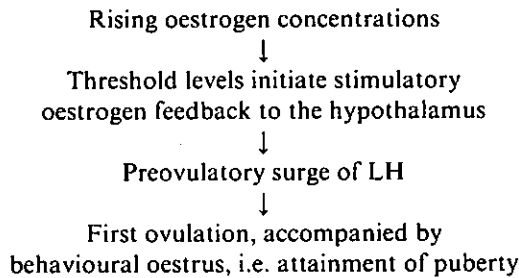
In summary, the current state of knowledge suggests that the boar effect operates via a synergistic action of several boar component stimuli. These include salivary and urinary pheromones (both identified and non-identified), tactile cues and, possibly, visual and auditory stimuli.

Mechanisms of action of the boar effect

At this point it would be ideal to relate the foregoing discussion to an endocrine mechanism for puberty attainment in the gilt. Unfortunately, the endocrine events leading to puberty attainment in the female are incompletely understood, even in those laboratory animals towards which most of the research effort has been directed. Nevertheless, many of the hormonal changes that occur in the prepubertal gilt can now be explained and a tentative scheme for sexual development may be outlined.

Endocrine development in the prepubertal period

Attainment of puberty in the gilt is normally defined as the time of first ovulation (Hughes, 1982; Paterson, 1982). The major endocrine changes occurring in the immediate prepubertal period that result in this ovulation are reasonably well documented (Karlhom *et al.*, 1981/2; Esbenshade *et al.*, 1982; Andersson *et al.*, 1983; Camous *et al.*, 1985), and may be represented as follows:



These changes are equivalent to endocrine profiles seen during the follicular phase of cyclic gilts (Esbenshade *et al.*, 1982). However, while the stimuli that initiate this follicular phase during the oestrous cycle are relatively well understood (Foxcroft & van de Wiel, 1982), this is not the case in the prepubertal gilt.

Since rising oestrogen concentrations imply that follicular growth is occurring, the most obvious stimulus for the gilt to enter this pro-oestrous phase would be an increase in gonadotrophin secretion. Such a change could be brought about by one or more of the following developmental changes:

- (1) a reduction in the sensitivity of the hypothalamic-pituitary unit to the inhibitory effects of oestradiol, i.e. the gonadostat theory (Ramirez & McCann, 1963; Grumbach *et al.*, 1974);
- (2) a reduction in the relative metabolic clearance rate of oestrogens (Elsaesser *et al.*, 1982; Christenson *et al.*, 1985);
- (3) increased GnRH output from the hypothalamus (Lutz *et al.*, 1985);
- (4) increased pituitary sensitivity to GnRH (Elsaesser & Smidt, 1986).

Alternatively, it has also been proposed that plasma oestrogen concentrations may rise as a result of changes in ovarian gonadotrophin receptors and/or steroidogenesis (Suzuki *et al.*, 1978; Smith-White & Ojeda, 1981; Meijs-Roelofs *et al.*, 1983). A further possibility is that a change occurs in the pattern of LH secretion such that, while the mean plasma concentration of this hormone remains unchanged, the pulse frequency increases and pulse amplitude decreases (Diekman *et al.*, 1983; Lutz *et al.*, 1984; Elsaesser & Smidt, 1986). The fact that either pulsatile administration of GnRH (Lutz *et al.*, 1985; Carpenter & Anderson, 1985) or exogenous LH (Huff & Esbenshade, 1988) is capable of stimulating precocious puberty in gilts would indicate that the final developmental event leading to onset of puberty occurs at the level of the hypothalamus.

The limited data available on endocrine profiles in the gilt during the weeks leading up to puberty attainment preclude the drawing of firm conclusions regarding the mechanisms that

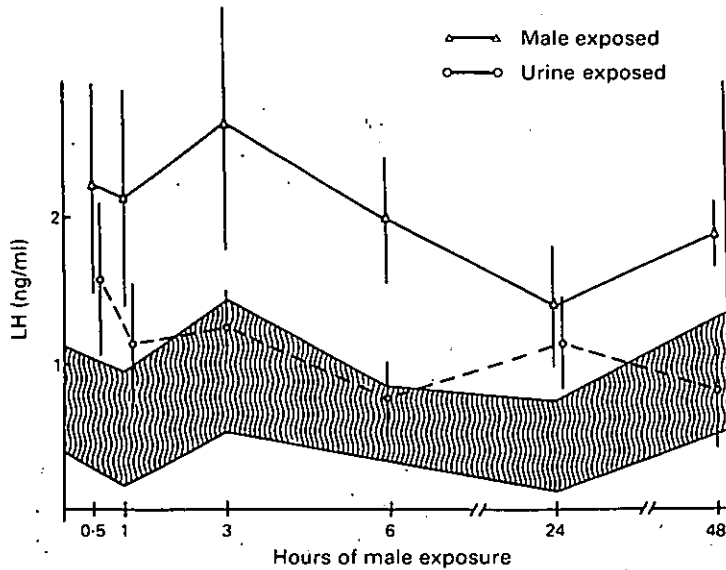


Fig. 1. Mean (\pm s.e.; 140–160 females/treatment) concentrations of serum LH in immature female mice exposed to male urine or to the presence of an intact male (from Bronson & Maruniak, 1976). The shaded area indicates the mean \pm s.e. for isolated controls.

initiate the first follicular phase; and hence puberty. Most reports suggest that the gilt is in a 'plateau' phase at this time, having low circulating concentrations of both gonadotrophins and oestradiol (Karlbom *et al.*, 1981/82; Andersson *et al.*, 1983; Diekman *et al.*, 1983), although the results of Lutz *et al.* (1984) indicated that plasma LH values may rise as early as 12 days before the gilt attains puberty. In addition, Camous *et al.* (1985) reported that oestrogen secretion may increase over a period of several weeks before attainment of puberty.

Endocrine responses of the gilt to boar contact

Paterson (1982) reviewed the known endocrine responses of gilts to boar contact and concluded that boars stimulate puberty in gilts by effecting a rise in oestradiol concentrations. What could not be determined at the time was the sequence of endocrine events that caused this elevation in plasma oestradiol values.

Studies on the male effect in rodents have revealed that male contact causes a rise in basal LH concentrations in the female (Bronson & Desjardins, 1974; Bronson & Maruniak, 1976). This is followed by a period of elevated plasma oestradiol concentrations that may last for as long as 2 days, and is thought to trigger a positive feedback response resulting in the preovulatory surge in gonadotrophin secretion. A similar LH response to male contact has also been reported in the ewe (Martin *et al.*, 1980).

Most studies of the gilt have failed to detect a significant change in the pattern of LH secretion in response to boar contact, although raised oestradiol concentrations have been observed (Paterson *et al.*, 1980; Esbenschade *et al.*, 1982; Andersson *et al.*, 1983). It is possible that a subtle change in LH concentrations may be induced by boar contact, or that changes occur in the magnitude and/or frequency of tonic LH release. The latter suggestion is supported by the work of Lutz *et al.* (1984) and would indicate an endocrine response to male contact similar to that seen in the ewe (Martin *et al.*, 1980; Poindron *et al.*, 1980). Such changes are difficult to detect in the gilt since normal circulating concentrations are extremely low and the interval from first boar contact

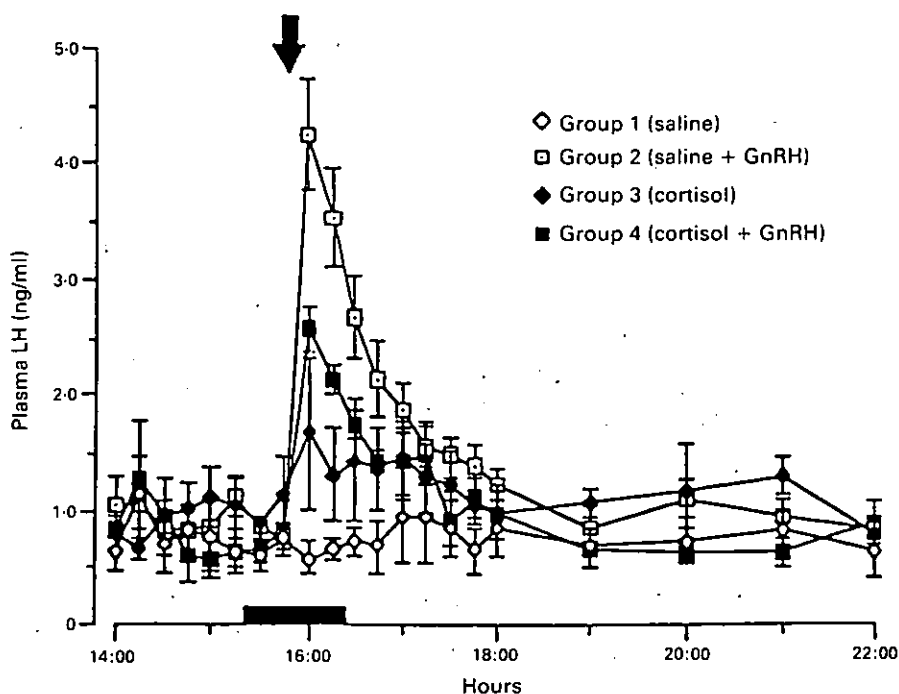


Fig. 2. The effects of cortisol infusion (horizontal bar) and GnRH administration (arrow) on LH secretion in the prepubertal gilt. Values are means \pm s.e.m. for 6 gilts/group. (From Pearce *et al.*, 1988.)

to puberty is so variable. The latter point is particularly relevant since it creates uncertainty as to when to impose a regimen of frequent blood collection to determine endocrine responses.

Exposure of prepubertal female rodents to male urine (the source of the primer pheromone in these species) in the absence of the male results in a reduced pubertal response (Bronson & Maruniak, 1975) and an abated LH response (Bronson & Maruniak, 1976; Fig. 1). Bronson & Maruniak (1976) also suggested that the role of the tactile cues from the males was to enhance the LH response of the females to male pheromones.

The tactile stimulation involved in boar contact is associated with an acute release of cortisol in the gilt (Pearce & Hughes, 1987a). This response is also seen when pigs are transported (Barnett *et al.*, 1984), relocated (Wodzicka-Tomaszewska *et al.*, 1985) or mated (Barnett *et al.*, 1982). Since a similar response can be obtained when gilts are exposed to a long-term androgenized castrated boar, this effect is clearly independent of olfactory stimulation (Pearce & Hughes, 1987a).

Whether or not this acute elevation in cortisol concentrations in response to boar exposure plays a role in boar-induced precocious puberty in gilts is equivocal. However, the fact that the removal of the tactile component from boar exposure (by using fence-line contact) reduces the efficacy of the boar effect strongly suggests that acute cortisol release may be a component of overall boar stimulation.

The interactions that occur between plasma cortisol and the gonadotrophic hormones appear to be complex. The fact that adrenalectomy reduces the pubertal response of gilts to boar exposure (Killian *et al.*, 1987) and to PMSG/hCG treatment (Killian *et al.*, 1983) suggests a stimulatory role for adrenal function in puberty attainment in the gilt. On the other hand, several studies have indicated that the administration of cortisol or ACTH decreases pituitary responsiveness to exogenous GnRH (Barb *et al.*, 1982; Fonda *et al.*, 1984; Pearce *et al.*, 1988). However, while acutely elevated cortisol concentrations reduced pituitary release of LH in response to exogenous GnRH

administration, they appeared to increase basal LH secretion (Li, 1987; Pearce *et al.*, 1988; Fig. 2). This elevation in basal LH levels may be associated with the commencement of follicular development and hence represent the important physiological response of the gilt to the tactile cues emanating from the boar.

Our current state of knowledge is insufficient to allow a full mechanism of action of the boar effect to be derived from the foregoing discussion. Nevertheless, a tentative scheme of endocrine responses to the boar may be suggested.

- (1) Boar pheromones may alter the pattern of LH secretion in the gilt (yet to be demonstrated).
- (2) The release of cortisol accompanying full boar contact further alters the secretory pattern of LH and/or physical contact with the boar enhances the transfer of primer pheromones.
- (3) These alterations in LH secretion stimulate follicular development and result in an elevation of plasma oestradiol concentrations.
- (4) The oestradiol stimulatory feedback system is triggered, resulting in the first preovulatory LH surge and thus the pubertal ovulation.

Conclusions

Our knowledge of the boar effect has been expanded to encompass its interactions with other factors that affect puberty attainment and those variations in its application that influence its efficacy. Furthermore, it is now established that the stimuli emanating from the boar are in two categories, namely olfactory and tactile/stress cues.

The endocrine basis of the boar effect remains obscure. While raised oestradiol concentrations are considered to be a consequence of boar exposure, other hormonal responses have yet to be consistently demonstrated. It is clear that the endocrine stimulus for follicular development, and hence oestradiol secretion, needs to be identified. Furthermore, the relationship between this stimulus and boar-originating cues must be established.

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