

FACTORS AFFECTING THE NATURAL ATTAINMENT OF PUBERTY IN THE GILT

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Puberty attainment in the gilt represents the onset of reproductive capability, since the first behavioural oestrus normally coincides with the pubertal ovulation. In the wild pig this first oestrus would occur in the late autumn when the gilt is approximately eight months of age (Signoret, 1980). However, in the domestic gilt the aim should be to stimulate the precocious attainment of puberty, the gilt being first mated, at second oestrus, at about 200 days of age.

It is both desirable and necessary to induce early puberty attainment in the gilt as she is a costly non-productive animal until the initiation of the first pregnancy. Thus, a review of the major factors influencing puberty attainment in the gilt is of value in identifying those measures which may be taken to reduce pubertal age and hence minimize the cost of introducing replacement gilts.

Factors influencing puberty attainment

AGE, LIVEWEIGHT AND RATE OF GROWTH

Several recent reviews have considered the relationship between puberty attainment and the age, liveweight and growth rate of the gilt (Hughes and Varley, 1980; Kirkwood, 1980). In each case the three factors were considered together as they are intimately related. In view of this it is difficult to dissociate the effects of each individual factor. Furthermore, in addition to having possible influences on puberty attainment themselves, they also reflect the effects of both genotype and nutrition. Thus, rather than review the effects of chronological age and liveweight on puberty attainment *per se* it is more useful to consider which of the two provides the more accurate reflection of the stage of development of the gilt. This measure of physiological development (often referred to as the physiological age) is used to assess the degree of maturity of the hypothalamic-pituitary-ovarian axis, and hence the ability of the gilt to respond to puberty stimulation.

Many reports suggest that gilts normally attain puberty at approximately 200–210 days of age (Duncan and Lodge, 1960; Anderson and Melampy, 1972). However, since the range in age at puberty can be as wide as 102

days (Aherne *et al.*, 1976) to 350 days and above (Brooks and Smith, 1980) the average figure appears to be of little value. Equally, gilt liveweight at puberty is extremely variable, reported pubertal weights varying from 55 kg (Aherne *et al.*, 1976) to over 120 kg (Hughes and Cole, 1975).

Despite this variability it has been reported repeatedly that chronological age is a more accurate indicator of degree of development than is liveweight (Robertson *et al.*, 1951a; Robertson *et al.*, 1951b; Duncan and Lodge, 1960; Hughes and Cole, 1976). It appears that the variability in gilt response to external stimuli (particularly boar contact) is greater at a constant liveweight than at a constant chronological age (Hughes and Cole, 1976).

There can be little doubt that many of the above data reflect the influences of many intrinsic and extrinsic factors, such as genotype, environment and boar contact, on puberty attainment. Nevertheless, they serve to illustrate the shortcomings of using either chronological age or liveweight as an indicator of a gilt's stage of development. Despite this, the consensus of opinion would appear to favour chronological age as the best available indicator of the physiological age of a gilt. Indeed, most studies on the effects of imposed stimuli on puberty attainment in the gilt have used a constant chronological age as the starting point for the stimulation. If the consensus of opinion is correct then the implication is that, under conventional feeding systems, the influence of nutrition on puberty attainment is minimal—otherwise the liveweight of the gilt would provide the better measure of physiological development. However, although this latter point remains in doubt (see below) it is reasonable to suggest that there exists a lower liveweight threshold below which gilts will not achieve puberty (Dickerson, Gresham and McCance, 1964).

If liveweight does exert little influence on puberty attainment it might also be supposed that the rate of liveweight increase, or growth rate, would also have a minimal effect on the timing of puberty. Many reports do suggest that this is the case in the gilt (Burger, 1952; Haines, Warnick and Wallace, 1959; Gossett and Sorensen, 1959; Sorensen, Thomas and Gossett, 1961; Goode, Warnick and Wallace, 1965), although this is not necessarily true in all species (Brody, 1945; Monteiro and Falconer, 1966). Despite this conclusion Reutzel and Sumption (1968) have demonstrated that a positive genetic relationship exists between age and puberty and daily liveweight gain in the gilt. These data imply that, while genotype may influence puberty attainment, variations in growth rate of animals of similar genotype will have little effect on puberty.

NUTRITION

Whilst it has been shown that both liveweight and growth rate may, under normal conditions, exert little influence on puberty attainment in the gilt, it must be emphasized that this conclusion is rather tenuous. Since both factors may reflect the nutrient supply to the animal it may be easier to reach more positive conclusions through studying the effects of variations in feed supply on puberty attainment. Thus, the relationships between the attainment of puberty and both plane of feeding and dietary composition are considered here.

Plane of feeding

Many early experiments to elucidate nutritional effects on reproduction in the pig used full- and limited-feeding systems as the basis for the studies. This means that the dietary regimes compared contained different levels of both energy and protein. Therefore, this work must be considered separately from the more recent investigations of energy and protein effects which have employed isonitrogenous and isoenergetic diets respectively.

The results available from these studies are both variable and conflicting. Several workers have reported that full feeding of prepubertal gilts results in the early attainment of puberty when compared with their restricted-fed counterparts (Burger, 1952; Zimmerman *et al.*, 1960; Goode, Warnick and Wallace, 1965; Friend, 1974; 1976). However, other results suggest that puberty attainment is either unaffected by plane of feeding (Robertson *et al.*, 1951b; Christian and Nofziger, 1952; Lodge and MacPherson, 1961, Pay and Davies, 1973) or is delayed by full feeding (Self, Grummer and Casida, 1955; Hafez, 1960; MacPherson, Hovell and Jones, 1977). These results are summarized in *Table 6.1*.

Table 6.1 THE EFFECTS OF PLANE OF NUTRITION ON PUBERTY ATTAINMENT IN GILTS

Age at puberty (days)		Source
High plane diet	Low plane diet	
198	203	Robertson <i>et al.</i> (1951b)
188	235	Burger (1952)
170	167	Christian and Nofziger (1952)
223	208	Self <i>et al.</i> (1955)
195	217	Haines <i>et al.</i> (1959)
212	182	Hafez (1960)
195	205	Zimmerman <i>et al.</i> (1960)
178	176	Lodge and MacPherson (1961)
262	292	Goode <i>et al.</i> (1965)
189	187	Pay and Davies (1973)
184	201	Friend (1974)
173	194	Friend (1976)
203	186	MacPherson <i>et al.</i> (1977)

The fact that significant results have been obtained to show that high plane feeding can both stimulate and inhibit puberty attainment suggests that other factors may also have been involved to confound the results. Indeed, both breed and seasonal effects are apparent in several of the experiments (e.g. Zimmerman *et al.*, 1960). More importantly, many of the experiments used boars for oestrus detection, hence introducing a further stimulatory influence (e.g. Robertson *et al.*, 1951b; Christian and Nofziger, 1952; Self, Grummer and Casida, 1955; Haines, Warnick and Wallace, 1959; Zimmerman *et al.*, 1960; Goode, Warnick and Wallace, 1965; Pay and Davies, 1973; MacPherson, Hovell and Jones, 1977). Since breed, season and boar contact are all known to influence puberty attainment, the interpretation of the above results must be questioned. Until such time as the interactions between plane of nutrition and these other stimulatory influences are understood no definite conclusion can be reached on the effects of feed level on puberty attainment in gilts.

Energy intake

The relationship between energy intake and puberty attainment in the gilt has been extensively reviewed by Anderson and Melampy (1972) and, more recently, by Hughes and Varley (1980). It was apparent in 1972 that no definite relationship between the two factors could be established on the basis of the available data. Indeed, Anderson and Melampy (1972) concluded from 14 experiments that restricted energy intake delayed puberty by an average of 16 days in nine experiments, whereas the restricted diet hastened the onset of puberty by 11 days in five other experiments (see *Table 6.2*).

Table 6.2 THE EFFECTS OF ENERGY INTAKE ON PUBERTY ATTAINMENT IN GILTS

Number of trials	ME intake (MJ/day)		Pubertal age (days)		Pubertal bodyweight (kg)	
	Restricted	Full	Restricted	Full	Restricted	Full
9	23.2	37.5	217	201	74	91
5	25.2	37.5	201	212	74	94

From Anderson and Melampy (1972).

Unfortunately, more recent studies do not clarify the situation. In fact, in four experiments studying the effects of energy intake on puberty attainment in the gilt, three concluded that no influence was apparent (Aherne *et al.*, 1976; Friend, 1977; Friend *et al.*, 1979) whereas the fourth suggested that a high energy intake resulted in a delayed onset of puberty (Etienne and Legault, 1974).

Once again these results are undoubtedly confounded by other stimuli, such as boar contact (Gossett and Sorensen, 1959; Sorensen, Thomas and Gossett, 1961; Friend, 1977; Friend *et al.*, 1979). Equally, factors such as degree of energy restriction, gilt age at the start of restriction, and dietary composition may have influenced the results. Hughes and Varley (1980) suggested that the restricted energy intakes used in many of the above studies were, in fact, adequate for an acceptable rate of growth. On this basis it may be expected that little effect would be seen on puberty attainment until a more severe level of restriction was imposed. Indeed, when Burger (1952) severely restricted energy intake (to 50% of *ad libitum*) puberty attainment was delayed by 46 days.

It seems that little progress has been made since Anderson and Melampy reviewed the situation in 1972. Nevertheless, it is reasonable to assume that puberty attainment will not be adversely affected by the levels of dietary energy being fed in practice, providing these contain sufficient energy to ensure an adequate level of liveweight growth.

Fat intake

Little information is available on the effects of dietary fat on puberty attainment in the gilt. It is generally assumed that fat will exert an influence only through its contribution to the total energy content of the diet. However, Witz and Beeson (1951) have reported that puberty attainment

is delayed in gilts fed fat-free diets. What remains to be established is whether this effect was due to dietary energy level or to a specific fat requirement by the gilt.

Protein intake

So far it has been assumed that the variations in gilt age at puberty as a result of plane of feeding were due to variations in energy intake. However, since protein intake would also vary with plane of feeding the effects of protein intake and aminoacid balance on puberty attainment must also be considered.

Several reports show that pubertal age increases when gilts are fed a protein-deficient diet (Davidson, 1930; Baker, 1959; Adams *et al.*, 1960; Cunningham *et al.*, 1974; Wahlstrom and Libal, 1977). On the other hand, minor variations in protein intake, in diets containing conventional levels of protein, do not appear to affect puberty attainment significantly (Friend, 1977; Friend *et al.*, 1979).

Fowler and Robertson (1954) reported that gilts fed protein of animal origin reached puberty significantly earlier than counterparts fed plant protein. This suggests that aminoacid imbalances in the diet may influence puberty attainment. Indeed, more recent evidence substantiates this, dietary supplementation with lysine and methionine reducing gilt age at puberty (Larsson, Nilsson and Olsson, 1966; Friend, 1973).

Vitamin and mineral intake

The roles of vitamins and minerals in pig reproduction generally, and puberty attainment in particular, have received very little attention. However, it does seem probable that severe restrictions of many vitamins and minerals, including vitamin A (Hughes, 1934), vitamin B₁₂ (Johnsen, Moustgaard and Højgaard-Olsen, 1952) and manganese (Plumlee *et al.*, 1956), may delay sexual development.

Overall, it has been suggested that nutrient supply, when sufficient for commercially acceptable growth rates, is unlikely to have any significant influence on puberty attainment in the gilt (Tassell, 1967; Brooks and Cole, 1974).

GENETICS

Ramirez (1973) states that 'the ontogeny of puberty is genetically determined for each species, but the normal rate of maturation can be altered by the environment and this can modify the stage of development'. This implies that genotype will exert a considerable influence on puberty attainment in gilts, although this influence may be masked by environmental stimuli.

Several workers have detected breed differences in age at puberty in the pig (Phillips and Zeller, 1943; Self, Grummer and Casida, 1955; Etienne

and Legault, 1974; Christenson and Ford, 1979). However, the variability in pubertal age within a breed is considerable, this being cited as a reason why other workers have failed to find significant breed differences (Robertson *et al.*, 1951a,b; Warnick *et al.*, 1951; Zimmerman *et al.*, 1960) – see Table 6.3. This within-breed variability in pubertal age may reflect the effects of other stimulatory influences (e.g. boar contact). Additionally, Christenson and Ford (1979) have concluded that significant breed–environment interactions may also exist, these only serving to further confound the situation. Thus, as in previous sections, the conflicting nature of the data prohibits the drawing of useful conclusions.

Table 6.3 THE EFFECTS OF BREED ON PUBERTY ATTAINMENT IN THE GILT

<i>Source</i>	<i>Breed used</i>	<i>Age at puberty (days)</i>
Robertson <i>et al.</i> (1951a)	Chester White	203
	Poland China	198
Robertson <i>et al.</i> (1951b)	Chester White	201
	Poland China	204
Warnick <i>et al.</i> (1951)		
	Trial 1	
	Chester White	236
	Yorkshire	243
Trial 2	Chester White	259
	Yorkshire	249
Self <i>et al.</i> (1955)		
	Trial 1	
	Chester White	225
	Poland China	206
	Trial 2	
Zimmerman <i>et al.</i> (1960)	Chester White	211
	Poland China	216
	Chester White (restricted-fed)	198
	Poland China (restricted-fed)	192
	Chester White (full-fed)	206
	Poland China (full-fed)	204
	Yorkshire	199
	Lacombe	197
Dyck (1971)		
	Landrace	173
Christenson and Ford (1979)	Large White	211
	Hampshire	207
	Duroc	224
	Yorkshire	221

In contrast, heterotic effects on puberty attainment in the gilt have been repeatedly and consistently demonstrated. The data presented in Table 6.4 clearly show that the crossbred gilt attains puberty earlier than its purebred counterpart. Such heterotic effects are not, however, confined to crosses between breeds. Foote *et al.* (1956), studying Chester White, Yorkshire and Chester White × Yorkshire gilts, reported that mean age at puberty was significantly reduced in line-cross gilts when compared with inbred gilts (194 versus 228 days respectively).

Most reproductive traits that show heterosis tend to be of low heritability. Indeed, Reutzel and Sumption (1968) have reported that the heritability of pubertal age is low or zero, when assessed on a paternal half-sib

Table 6.4 THE DIFFERENCE IN PUBERTAL AGE BETWEEN PUREBRED AND CROSSBRED GILTS

Source	Breed of sire	Breed of dam	Difference in pubertal age between crossbred gilts and their purebred counterparts (days)
Warnick <i>et al.</i> (1951)	Trial 1: Chester White	Yorkshire	—4
	Trial 2: Chester White	Yorkshire	—3
Foote <i>et al.</i> (1956)	Poland China	Duroc	—11
	Poland China	Yorkshire	—32
	Duroc	Yorkshire	—36
Short <i>et al.</i> (1963)	Duroc	Yorkshire	—10
	Yorkshire	Duroc	—5
Clark <i>et al.</i> (1970)	Poland China	Yorkshire	—24
	Yorkshire	Poland China	—6

analysis. However, these workers did obtain a heritability estimate of 0.49 when a daughter–dam regression was used. Such data may reflect a dam effect on the pubertal age of offspring. Other workers have also noted family effects (Burger, 1952) and, particularly, sire effects on gilt age at puberty (Reddy, Lasley and Mayer, 1958; Short, 1963; Hughes and Cole, 1975). Hence, while a reliable figure for the heritability of pubertal age is not available, there would appear to be some genetic basis for selection of this trait.

CLIMATIC ENVIRONMENT

Although the domestic pig does not have a specific breeding season, it is derived from a seasonally breeding animal and might therefore be expected to show variations in fertility with time of year.

Many reports suggest that season of birth exerts a marked effect on puberty attainment in the gilt. Unfortunately, many of these data are conflicting (Table 6.5), some reports indicating that autumn-born gilts reach puberty earlier than their spring-born counterparts (Wiggins, Casida and Grummer, 1950; Gossett and Sorensen, 1959; Mavrogenis and Robison, 1976) while others indicate the reverse (Sorensen, Thomas and

Table 6.5 THE EFFECTS OF SEASON OF BIRTH ON PUBERTY ATTAINMENT IN THE GILT

Source	No. of gilts	Age at puberty (days)	
		Spring-born	Autumn-born
Gossett and Sorensen (1959)	52	216	206
Zimmerman <i>et al.</i> (1960)			
Trial 1	71	196	208
Trial 2	60	203	190
Sorensen <i>et al.</i> (1961)	98	210	208
Mavrogenis and Robison (1976)	153	237	202

Gossett, 1961; Scanlon and Krishnamurthy, 1974). Other studies have either failed to observe seasonal differences at all (Wise and Robertson, 1953; Self, Grummer and Casida, 1955; Christenson and Ford, 1979), found significant differences in one year but not the next (Warnick *et al.*, 1951), or found significant differences in only one of two breeds (Zimmerman *et al.*, 1960). Such inconsistent results must, once again, be reflections of stimulatory influences other than those associated with season. Thus, although it might be expected that spring-born gilts would mature earlier, as did their wild ancestors (Signoret, 1980), there is little evidence to substantiate this. Additionally, it is not clear that puberty attainment in the wild gilt is in response to seasonal changes, since boar contact is also initiated in the autumn.

Table 6.6 THE EFFECTS OF PHOTOPERIOD ON PUBERTY ATTAINMENT IN THE GILT

Source	No. of gilts	Lighting regime	Age at puberty (days)
Dufour and Bernard (1968)	—	complete darkness	208
	—	natural photoperiod	219
Hacker <i>et al.</i> (1974)	16	complete darkness	222
	16	12 hours light:12 hours dark	183
Hacker <i>et al.</i> (1976)	16	6 hours light:18 hours dark	232
	16	18 hours light:6 hours dark	190
Hacker <i>et al.</i> (1979)	6	complete darkness	200
	6	natural photoperiod	
	6	(9.0–10.8 hours light per day)	165
Ntunde <i>et al.</i> (1979)		18 hours light:6 hours dark	175
	12	complete darkness	193
	12	natural photoperiod	
		(9.0–10.8 hours light per day)	176
	12	18 hours light:6 hours dark	177

Seasonal differences will reflect changes in both photoperiod and temperature. It is therefore worthwhile to consider the effects of these two factors in isolation. Most studies (*Table 6.6*) on photoperiod demonstrate that increasing daylength advances the onset of puberty in gilts (Martinat *et al.*, 1970; Surmuhiin and Ceremnyh, 1970; Surmuhiin *et al.*, 1970; Hacker, King and Bearss, 1974; Hacker, King and Smith, 1976; Hacker *et al.*, 1979; Ntunde, Hacker and King, 1979). The one conflicting report is that of Dufour and Bernard (1968) who found that gilts reared in complete darkness reached puberty earlier than those reared in normal daylength. While this result agrees with data from other species (e.g. Zacharias and Wurtman, 1964), the rearing of gilts in complete darkness is an abnormal situation that is likely to yield abnormal results. Thus, it may be concluded that long daylengths will be conducive to the early maturation of gilts. The actual optimum light:dark schedule has not been elucidated, although the available data (Klotchkov, Klotchkova, Kim and Belyaev, 1971; Hacker, King and Smith, 1976; Hacker *et al.*, 1979; Ntunde, Hacker and King, 1979) does indicate that 17–18 hours light/day should be sufficient.

The effects of temperature on puberty attainment in gilts are less well documented. High environmental temperatures have been reported to exert an adverse influence on several aspects of reproduction in pigs

(Corteel, Signoret and Du Mesnil du Buisson, 1964; Edwards *et al.*, 1968; Teague, Roller and Griffio, 1968; Love, 1978), with limited evidence indicating that this may also be true for puberty attainment (Schmidt and Bretschneider, 1954; Stickney *et al.*, 1978). Conversely, Dyck (1974) has observed that the rearing of gilts under conditions of low environmental temperatures has no adverse influence on the attainment of puberty. It may be concluded that moderately low environmental temperatures will facilitate the early attainment of puberty in the gilt. However, it is also worth applying a note of caution, since work with other species has indicated that both very high and very low temperatures may delay the attainment of sexual maturity (Mandl and Zuckerman, 1952; Donovan and van der Werff ten Bosch, 1965).

When the data on photoperiod and temperature are combined to provide seasonal effects it is not surprising that variations in pubertal age are not consistent. Spring-born gilts will be stimulated to reach puberty early by the increasing daylength, but will be inhibited by high environmental temperatures. Conversely, autumn-born gilts will be stimulated by lower temperatures but inhibited by short daylengths. Thus, the actual location of the experimental site (together with the environmental control of the building, where applicable), and hence the actual temperatures and photoperiod experienced by the gilts, will, to a large extent, determine the response obtained.

SOCIAL ENVIRONMENT

It has long been known that 'stress' factors may both stimulate and inhibit puberty attainment in rodents, the response being dependent on the type and level of 'stress' applied (Duckett, Varon and Christian, 1963; Morton, Denenberg and Zarrow, 1963). In the gilt there is also limited evidence to indicate that some forms of 'stress' may stimulate the early attainment of puberty.

Table 6.7 THE EFFECTS OF STOCKING DENSITY ON PUBERTY ATTAINMENT IN THE GILT

Source	No. of gilts	No. of gilts/pen	Age at puberty (days)	
Jensen <i>et al.</i> (1970) ^(a)	—	1	260	
		5–7	262	
		6–10	261	
Robison (1974)	15	1	225	
	30	30	216	
Mavrogenis and Robison (1976)	50	1	222	
	103	30	207	
Ford and Teague (1978) ^(b)	32	8	217	
	96	12	199	
Christenson and Ford (1979)	Trial 1	31	8	206
		48	24	207
	Trial 2	32	8	247
		46	24	253

^(a)Data averaged from three trials

^(b)Data from three trials where space restriction was also varied.

Several workers have reported that the crowding of gilts will stimulate early sexual maturation (Robison, 1974; Mavrogenis and Robison, 1976), although other workers have found no effect (Jensen *et al.*, 1967, 1970; Christenson and Ford, 1979). These data are summarized in *Table 6.7*. What is not clear at present is whether crowding effects, if they exist, are mediated through space restriction (a form of 'stress') or through the presence of many other females (Ford and Teague, 1978).

Undoubtedly, the best known 'stress' factor in pigs is that of transportation. Many workers have reported that transporting prepubertal gilts will result in the precocious attainment of puberty (Du Mesnil du Buisson and Signoret, 1961; Paredis, 1961; Signoret, 1970). However, this stimulus may not be effective until the gilt is very near puberty, since Signoret (1972) reported that only 26.5% of gilts weighing 90–110 kg responded to transportation. When this effect is apparent it is clearly independent of boar stimulation since the peak of oestrus occurrence is unaltered when boar exposure is delayed for 10 days after transportation (Signoret, 1970) as shown in *Figure 6.1*.

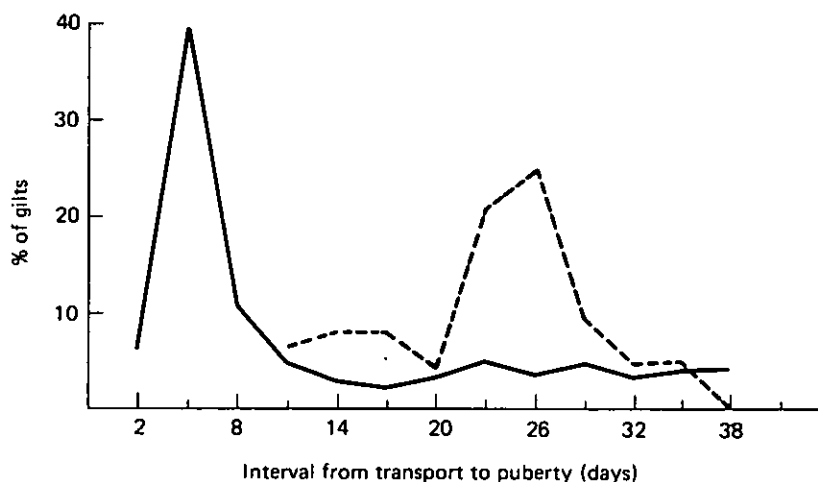


Figure 6.1 The interval between transport and the onset of oestrus in gilts. Dotted line indicates results when presentation to the boar is delayed for 10 days. From Signoret (1970)

The most recent studies in this area have concentrated on the interactions of mixing strange gilts, transportation and relocation, these being tested in the presence or absence of boar contact. The data on these 'management stresses', summarized in *Table 6.8* indicate that all these 'stress' factors may have stimulatory effects on puberty attainment in gilts. However, the results presented in *Table 6.8* also indicate that boar contact is a more potent form of puberty stimulation than is any form of 'stress'. Finally, it is worth noting that boar contact itself may also include a 'stress' component (Kirkwood, Forbes and Hughes, 1981).

BOAR CONTACT

It has already been pointed out that contact with a boar will induce puberty attainment in the prepubertal gilt. Indeed, this fact has been repeatedly

Table 6.8 THE EFFECT OF 'MANAGEMENT STRESS', WITH OR WITHOUT BOAR CONTACT, ON PUBERTY ATTAINMENT IN THE GILT

Source	No. of gilts	'Management stress'			Boar contact	Treatment age (days)	Age at puberty (days)
		Mixing ^(a)	Transport	Relocation			
Bourn <i>et al.</i> (1974)	—	—	—	—	+	135 or 165 days	167
Zimmerman <i>et al.</i> (1974)	34	+	+	—	+	135 or 165 days	161
	68	—	+	+	—	125, 150 or 175 days	204
Bourn <i>et al.</i> (1976)	44	—	+	+	+	125, 150 or 175 days	181
	44	+	+	+	—	135 or 165 days	193
Scheimann <i>et al.</i> (1976)	—	+	+	+	+	135 or 165 days	176
	—	+	—	—	—	—	(0%) ^(b)
	—	—	+	—	—	—	(26%)
	—	—	+	+	+	—	(79%)
Zimmerman <i>et al.</i> (1976)	25	+	+	+	+	—	(88%) ^(c)
	25	+	—	—	—	165 days	(7%) ^(c)
	25	+	+	—	—	165 days	(8%)
	25	+	+	+	—	165 days	(28%)
		+	+	+	+	165 days	(87%)

^(a)Mixing of strange gilts.^(b)Percentage of gilts reaching puberty within 17 days of the start of treatment.^(c)Percentage of gilts reaching puberty within 10 days of the start of treatment.

Table 6.9 THE EFFECTS OF GILT AGE AT FIRST BOAR CONTACT ON PUBERTAL AGE AND THE INTERVAL FROM FIRST BOAR CONTACT TO PUBERTY

<i>Source</i>	<i>Gilt age at boar introduction (days)</i>	<i>Interval from first boar contact to puberty (days)</i>	<i>Age at puberty (days)</i>
Zimmerman <i>et al.</i> (1969)	103	67	170
Zimmerman <i>et al.</i> (1974)	125	47	172
Kirkwood and Hughes (1979)	125	54	179
Zimmerman <i>et al.</i> (1969)	126	31	157
Kirkwood and Hughes (1979)	132	42	174
Bourn <i>et al.</i> (1974)	135	21	156
Hughes and Cole (1976)	135	34	169
Bourn <i>et al.</i> (1976)	135	40	175
Kirkwood and Hughes (1979)	139	27	166
Kirkwood and Hughes (1979)	146	21	167
Zimmerman <i>et al.</i> (1974)	150	32	182
Kirkwood and Hughes (1979)	153	28	181
Brooks and Smith (1980)	160	11	171
Paterson and Lindsay (1980)	160	15	175
Hughes and Cole (1976)	160	18	178
Kirkwood and Hughes (1979)	160	19	179
Brooks <i>et al.</i> (1969)	163	7	170
Brooks and Cole (1970)	165	7	172
Bourn <i>et al.</i> (1974)	165	8	173
Bourn <i>et al.</i> (1976)	165	13	178
Kirkwood and Hughes (1979)	167	12	179
Brooks and Cole (1969)	171	21	192
Kirkwood and Hughes (1979)	174	24	198
Zimmerman <i>et al.</i> (1974)	175	15	190
Kirkwood and Hughes (1979)	181	16	197
Brooks and Cole (1973)	183	16	199
Brooks and Cole (1973)	188	14	202
Hughes and Cole (1976)	190	15	205
Brooks and Smith (1980)	200	16	216
Brooks and Cole (1973)	215	10	225

demonstrated by many workers (Brooks and Cole, 1969; 1970; Brooks, Pattinson and Cole, 1969; Robison, 1974; Hughes and Cole, 1976; 1978; Mavrogenis and Robison, 1976; Thompson and Savage, 1978; Kirkwood and Hughes, 1979).

The major factor controlling the efficiency of boar contact as a puberty stimulus is the age of the gilt at the time of boar introduction. This is clearly shown in *Table 6.9* and *Figures 6.2* and *6.3*. When boar contact is initiated at very young gilt ages (3–4 months), pubertal response is minimal and sexual development may possibly be delayed (Zimmerman, Carlson and Nippert, 1969; Brooks and Cole, 1969; Doroshkov, 1974; Hughes and Cole, 1976). This is considered to reflect the relatively young physiological ages of these gilts at the time the stimulus is introduced. Consequently, it has been suggested by Brooks and Cole (1969) that the young gilt may become habituated to the boar stimulus at a stage in development when she is too young to respond. Thus, when the gilt reaches an age when a pubertal response to boar contact might be expected (see below), it is not forthcoming and puberty occurs at a similar age to that of unstimulated gilts.

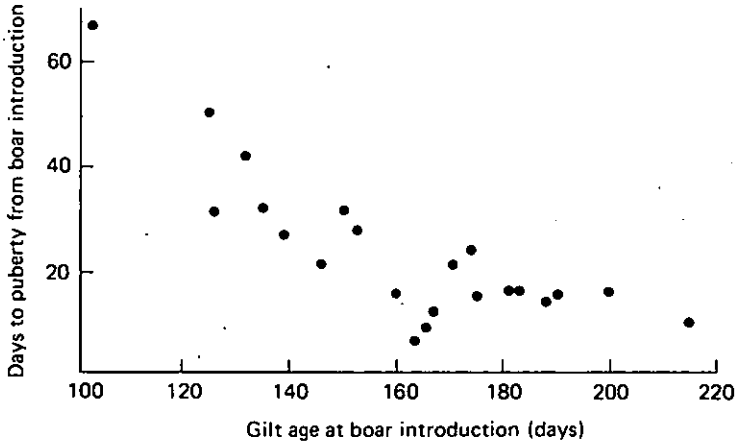


Figure 6.2 The relationship between gilt age at boar introduction and the interval from first boar contact to puberty (data relate to *Table 6.9*)

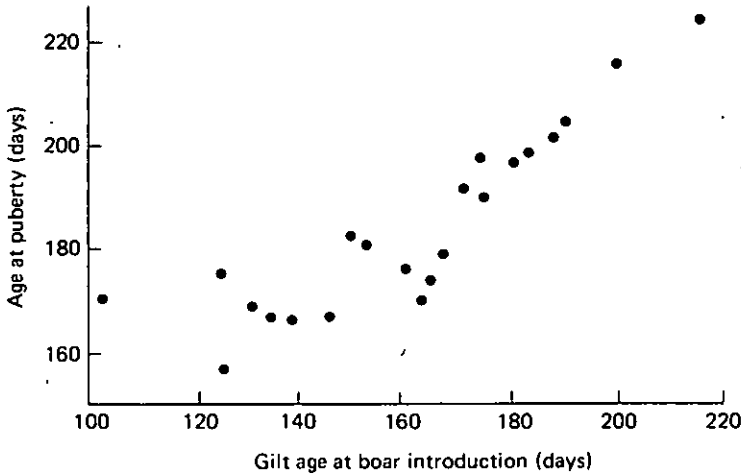


Figure 6.3 The relationship between gilt age at boar introduction and age at puberty (data relate to *Table 6.9*)

Conversely, when boar introduction is delayed until the immediate prepubertal period (six months of age and above) the response is again limited but for a different reason. When boar contact is initiated at these late gilt ages puberty attainment is stimulated, the interval from first boar contact to puberty being similar to that seen in gilts first stimulated at 160–165 days of age. However, by virtue of the relatively old ages of the gilts at boar introduction, the actual pubertal ages of these gilts are not much reduced below those of unstimulated animals.

While both very young and relatively old gilts demonstrate limited responses to boar contact, gilts first exposed to a boar at 150–170 days of age display a significant precocity in sexual development. Indeed, when boar introduction occurs at gilt ages in the region of 160 days, both the

interval from first boar contact to puberty and gilt age at puberty are minimized (*Figures 6.2 and 6.3*). Additionally, initiating boar contact at this age results in maximum synchronization of the pubertal oestrus (Brooks and Cole, 1970; Hughes and Cole, 1976).

A report by Brooks and Cole (1970) suggested that gilt response to boar introduction at about 160 days of age could be improved by employing a rotation of boars rather than contact with a single boar. However, several confounding factors present in this experiment prohibited the automatic acceptance of this result. Indeed, more recent studies, albeit using limited numbers of animals, have failed to substantiate the earlier claim. The results of these recent experiments (Kirkwood, 1980; Kirkwood and Hughes, 1980a) indicate that neither a rotation of boars nor continuous boar contact improve gilt response above that obtained with single boar contact for 30 minutes/day (*Table 6.10*).

Table 6.10 THE EFFECTS OF 30 MINUTES/DAY BOAR CONTACT, CONTINUOUS BOAR CONTACT AND ROTATIONAL BOAR CONTACT ON PUBERTY ATTAINMENT IN THE GILT

<i>Source</i>	<i>No. of gilts/ treatment</i>	<i>Gilt age at puberty (days)</i>		
		<i>30 min/day</i>	<i>continuous</i>	<i>rotational</i>
Kirkwood and Hughes (1980a)	10	199	195	—
Kirkwood (1980)	6	187	183	194

All boar contact was initiated at 165 days of age.

The actual mechanism by which boar contact stimulates puberty attainment in gilts has only recently been investigated. It has long been known that, in other species, this 'male effect' is mediated via a primer pheromone (Vandenbergh, 1969), this, in turn, stimulating an endogenous LH (luteinizing hormone) release in the recipient female (Bronson and Desjardins, 1974). In the pig it was unclear whether the male effect was due to a pheromone, or whether other boar stimuli such as 'stress', auditory and visual cues were involved. A recent experiment carried out by Kirkwood, Forbes and Hughes (1981) set out to investigate this problem by considering the ability of boars to stimulate puberty attainment in anosmic gilts. The results of this trial show that boar contact is ineffective in stimulating precocious puberty attainment in gilts that are unable to perceive pheromones (*Table 6.11*). This implies that the 'boar effect' is mediated via a primer pheromone. It should, however, be recognized that other boar-originating stimuli may act synergistically with the primer pheromone(s) to produce the complete 'boar effect'.

Table 6.11 THE INFLUENCE OF BOAR CONTACT^(a) ON PUBERTY ATTAINMENT IN INTACT AND OLFATORY BULBECTOMIZED GILTS

<i>Treatment</i>	<i>Interval from first boar contact to puberty (days)</i>	<i>Age at puberty (days)</i>
Control—no boar contact or surgery	74	234
Boar exposure—olfactory bulbectomized	70	230
Boar exposure—sham-operated	44	204
Boar exposure—no surgery	48	208

^(a)From 160 days of age.

From Kirkwood, Forbes and Hughes (1981).

The nature of the boar pheromone responsible for puberty stimulation has yet to be identified. The major free pheromones produced by the boar originate in the submaxillary salivary gland, and this is considered to be the most probable source of the puberty-accelerating pheromone (Booth, 1980; Kirkwood and Hughes, 1980b; Kirkwood, Forbes and Hughes, 1981). Indeed, it has been suggested that the active pheromone responsible for puberty induction is 3 α -androstenol, but this claim remains to be substantiated.

Most reproductively active pheromones produced by the boar are secreted at very low levels in the young boar, and do not rise to adult levels until the boar approaches one year of age (Booth, 1975). It is, therefore, necessary to consider whether the young postpubertal boar is capable of inducing precocious puberty attainment in the gilt. The one small trial that has been conducted on this subject (*Table 6.12*) indicated that the boar

Table 6.12 THE EFFECT OF EXPOSURE TO BOARS^(a) OF DIFFERENT AGES ON PUBERTY ATTAINMENT IN THE GILT

<i>Treatment</i>	<i>Interval from first boar contact to puberty (days)</i>	<i>Age at puberty (days)</i>
Control—no boar exposure	39	203
Exposure to 6.5-month old boar	42	206
Exposure to 11-month old boar	18	182
Exposure to 24-month old boar	19	182

^(a)30 minute daily exposure from an average gilt age of 164 days.
From Kirkwood and Hughes (1981).

may not be able to stimulate puberty attainment in the gilt until he is approximately 9–10 months of age (Kirkwood and Hughes, 1981). Thus, it may be suggested that older boars are used to induce puberty attainment in replacement gilts. Finally, since entire litter brothers would not be stimulatory to their sisters, it seems unlikely that mixed-sex rearing would result in an habituation effect in the gilt—a conclusion supported by the recent work of Nathan and Cole (1981).

Conclusions

It is apparent from the foregoing discussion that the rate of sexual development in gilts can be modified by many factors. However, it is equally clear that there has been a lack of definitive research to identify the influences of individual stimulatory/inhibitory factors on puberty attainment. The problem arises, in the main, as a result of using boars to detect the occurrence of the pubertal oestrus. Since it has already been demonstrated that boar contact is the single most effective puberty stimulus, it is difficult to assess the true influence of other factors being examined in such experiments. Whilst the boar contact may be applied over all treatments, and hence may be considered as a standard part of the experiment, it will certainly mask the influences of the applied variables (e.g. nutrition, genotype or climatic environment) and may also interact with them to

confound interpretation. In view of these problems, it has proved necessary to apply a note of caution when interpreting the majority of available data on factors influencing puberty attainment. Indeed, it is suggested that future experiments in this area should, with the exception of those studies aimed at elucidating aspects of the 'boar effect', avoid the use of boars for oestrus detection. It is recognized that such a move would make the detection of oestrus difficult but, equally, it would allow easier interpretation of results. Under such conditions oestrus detection may be carried out using one or more of three available methods. These are:

- (a) visual observations of vulval and behavioural changes,
- (b) regular blood sampling and the measurement of plasma progesterone concentrations, and
- (c) slaughter followed by ovarian examination for the presence of corpora lutea and corpora albicantia.

This system, using all three methods, has been applied to good effect by Hughes and Cole (1978), and has proved to be as effective (if not as simple) a method of oestrus detection as the use of a boar.

Finally, despite the reservations expressed above, it may be concluded that boar contact is the single most effective natural means of stimulating precocious puberty attainment in the gilt. Response to this stimulus may, however, be augmented by the additional imposition of 'social stress'. Under commercial conditions nutritional and climatic influences on sexual development should be minimal in temperate regions, although both are likely to exert adverse influences under sub-tropical and tropical conditions. Lastly, genotype differences may prove to be useful in a selection programme in the future, but, for the present, there is insufficient information available to justify such a programme.

References

- ADAMS, C.R., BECKER, D.E., TERRILL, S.W., NORTON, M.W. and JENSEN, A.H. (1960). Rate of ovulation and implantation in swine as affected by dietary protein. *J. Anim. Sci.* **19**, 1245 (Abstract)
- AHERNE, F.X., CHRISTOPHERSON, R.J., THOMPSON, J.R. and HARDIN, R.T. (1976). Factors affecting the onset of puberty, postweaning oestrus and blood hormone levels of Lacombe gilts. *Can. J. Anim. Sci.* **56**, 681-692
- ANDERSON, L.L. and MELAMPY, R.M. (1972). Factors affecting ovulation rate in the pig. In *Pig Production* (D.J.A. Cole, Ed.), pp. 329-366. London Butterworths
- BAKER, B. (1959). Effects of changing levels of nutrition on reproduction of gilts. *J. Anim. Sci.* **18**, 1160 (Abstract)
- BOOTH, W.D. (1975). Changes with age in the occurrence of C₁₉ steroids in the testis and submaxillary gland of the boar. *J. Reprod. Fert.* **42**, 459-472
- BOOTH, W.D. (1980). A study of some major testicular steroids in the pig in relation to their effect on the development of male characteristics in the pre-pubertally castrated boar. *J. Reprod. Fert.* **59**, 155-162
- BOURN, P., CARLSON, R., LANTZ, B. and ZIMMERMAN, D.R. (1974). Age at

- puberty in gilts as influenced by age at boar exposure and transport. *J. Anim. Sci.* **39**, 987 (Abstract)
- BOURN, P., KINSEY, R., CARLSON, R. and ZIMMERMAN, D.A. (1976). Puberty in gilts as influenced by boar exposure and "transport phenomenon". *J. Anim. Sci.* **41**, 344 (Abstract)
- BRODY, S. (1945). *Bioenergetics and Growth*. New York, Reinhold
- BRONSON, F.H. and DESJARDINS, C. (1974). Circulating concentrations of FSH, LH, oestradiol and progesterone associated with acute male-induced puberty in mice. *Endocrinology* **94**, 1658-1668
- BROOKS, P.H. and COLE, D.J.A. (1969). Effect of boar presence on the age at puberty of gilts. *Rep. Sch. Agric. Univ. Nott.* 74-77
- BROOKS, P.H. and COLE, D.J.A. (1970). Effect of the presence of a boar on attainment of puberty in gilts. *J. Reprod. Fert.* **23**, 435-440
- BROOKS, P.H. and COLE, D.J.A. (1973). Meat production from gilts which have farrowed. 1. Reproductive performance and food conversion efficiency. *Anim. Prod.* **17**, 305-315
- BROOKS, P.H. and COLE, D.J.A. (1974). The effect of nutrition during the growing period and the oestrous cycle on the reproductive performance of the pig. *Livest. Prod. Sci.* **1**, 7-20
- BROOKS, P.H., PATTINSON, M.A. and COLE, D.J.A. (1969). Reproduction in the young gilt. *Rep. Sch. Agric. Univ. Nott.* 65-67
- BROOKS, P.H. and SMITH, D.A. (1980). The effect of mating age on the reproductive performance, food utilisation and liveweight change of the female pig. *Livest. Prod. Sci.* **7**, 67-78
- BURGER, J.F. (1952). Sex physiology of pigs. *Onderstepoort J. vet. Res., Suppl.* **2**, 41-52
- CHRISTENSON, R.K. and FORD, J.J. (1979). Puberty and estrus in confinement-reared gilts. *J. Anim. Sci.* **49**, 743-751
- CHRISTIAN, R.E. and NOFZIGER, J.C. (1952). Puberty and other reproductive phenomena in gilts as affected by plane of nutrition. *J. Anim. Sci.* **11**, 789 (Abstract)
- CLARK, J.R., FIRST, N.L., CHAPMAN, A.B. and CASIDA, L.E. (1970) Age at puberty in four genetic groups of swine. *J. Anim. Sci.* **31**, 1032 (Abstract)
- CORTEEL, J.M., SIGNORET, J.P. and DU MESNIL DU BUISSON, F. (1964). Seasonal variations in the reproduction in the sow and factors favouring temporary anoestrus. *5th Int. Congr. Anim. Reprod. A.I., Trento*, **3**, 536-540
- CUNNINGHAM, P.J., NABER, C.H., ZIMMERMAN, D.R. and PEO, E.R. (1974). Influence of nutritional regime on age at puberty in gilts. *J. Anim. Sci.* **39**, 63-67
- DAVIDSON, H.R. (1930). Reproductive disturbances caused by feeding protein-deficient and calcium-deficient rations to breeding pigs. *J. agric. Sci., Camb.* **20**, 233-239
- DICKERSON, J.W.T., GRESHAM, G.A. and McCANCE, R.A. (1964). The effect of undernutrition and rehabilitation on the development of the reproductive organs: pigs. *J. Endocr.* **29**, 111-118
- DONOVAN, B.T. and VAN DER WERFF TEN BOSH, J.J. (1965). *Physiology of Puberty*. Monographs of the Physiological Society No. 15, London, Arnold

- DOROSHKOV, V.B. (1974). Stimulatory effect of males on reproductive performance of female pigs. *Anim. Breed Abstr.* **42**, 3830
- DUCKETT, G.E., VARON, H.H. and CHRISTIAN, J.J. (1963). Effects of adrenal androgens on parabiotic mice. *Endocrinology* **72**, 403-409
- DUFOUR, J. and BERNARD, C. (1968). Effect of light on the development of market pigs and breeding gilts. *Can. J. Anim. Sci.* **48**, 425-430
- DU MESNIL DU BUISSON, F. and SIGNORET, J.P. (1961). Influence des facteurs externes sur le déclenchement de la puberté chez la truie. *Ann. Zootech.* **11**, 53-59
- DUNCAN, D.L. and LODGE, G.A. (1960). Diet in relation to reproduction and viability of the young. *Comm. Bur. Anim. Nutr. Tech. Comm.* No. 21
- DYCK, G.W. (1971). Puberty, post-weaning estrus and estrus cycle length in Yorkshire and Lacombe swine. *Can. J. Anim. Sci.* **51**, 135-140
- DYCK, G.W. (1974). Effects of a cold environment and growth rate on reproductive efficiency in gilts. *Can. J. Anim. Sci.* **54**, 287-292
- EDWARDS, R.L., OMTVEDT, I.T., TURMAN, E.J., STEPHENS, D.F. and MAHONEY, G.W.A. (1968). Reproductive performance of gilts following heat stress prior to breeding and in early gestation. *J. Anim. Sci.* **27**, 1634-1637
- ETIENNE, M. and LEGAULT, C. (1974). Effects of breed and diet on sexual precocity in the sow. *Journées de la recherche porcine en France*, pp. 52-62. Paris, L'Institut Technique du Porc
- FOOTE, W.C., WALDORF, D.P., CHAPMAN, A.B. SELF, H.L., GRUMMER, R.H. and CASIDA, L.E. (1956). Age at puberty of gilts produced by different systems. *J. Anim. Sci.* **15**, 959-969
- FORD, J.J. and TEAGUE, H.S. (1978). Effect of floor space restriction on age at puberty in gilts and on performance of farrows and gilts. *J. Anim. Sci.* **47**, 828-832
- FOWLER, S.H. and ROBERTSON, E.L. (1954). Some effects of source of protein and an antibiotic on reproductive performance of gilts. *J. Anim. Sci.* **13**, 949-954
- FRIEND, D.W. (1973). Influence of dietary amino acids on the age at puberty of Yorkshire gilts. *J. Anim. Sci.* **37**, 701-707
- FRIEND, D.W. (1974). Pubertal age and composition of uterus in gilts. *J. Anim. Sci.* **39**, 975 (Abstract)
- FRIEND, D.W. (1976). Nutritional effects on age at puberty and plasma amino acid level in Yorkshire gilts and on chemical composition, nucleic acid, fatty acid and hydroxy proline content of the uterus. *J. Anim. Sci.* **43**, 404-412
- FRIEND, D.W. (1977). Effect of dietary energy and protein on age and weight at puberty of gilts. *J. Anim. Sci.* **44**, 601-607
- FRIEND, D.W., LARMOND, E., WOLYNETZ, M.S. and PRICE, K.R. (1979). Piglet and pork production from gilts bred at puberty: chemical composition of the carcass and assessment of meat quality. *J. Anim. Sci.* **49**, 330-341
- GOODE, L., WARNICK, A.C. and WALLACE, H.D. (1965). Effect of dietary energy levels upon reproduction and the relation of endometrial phosphatase activity to embryo survival in gilts. *J. Anim. Sci.* **24**, 959-963
- GOSSETT, J.W. and SORENSEN, A.M. (1959). The effect of two levels of energy and seasons on reproductive phenomena in gilts. *J. Anim. Sci.* **18**, 40-47

- HACKER, R.R., KING, G.J. and BEARSS, W.H. (1974). Effects of complete darkness on growth and reproduction in gilts. *J. Anim. Sci.* **39**, 155 (Abstract)
- HACKER, R.R., KING, G.J., NTUNDE, B.N. and NARENDHAN, R. (1979). Plasma estrogen, progesterone and other reproductive responses of gilts to photoperiod. *J. Reprod. Fert.* **57**, 447-451
- HACKER, R.R., KING, G.J. and SMITH, V.G. (1976). Effects of 6 and 18 hour light on reproduction in gilts. *J. Anim. Sci.* **43**, 228 (Abstract)
- HAFEZ, E.S.E. (1960). Nutrition in relation to reproduction in sows. *J. agric. Sci., Camb.* **54**, 170-178
- HAINES, C.E., WARNICK, A.C. and WALLACE, H.D. (1959). The effects of two levels of energy intake on reproductive phenomena in Duroc Jersey gilts. *J. Anim. Sci.* **18**, 347-354
- HUGHES, E.H. (1934). Some effects of vitamin A-deficient diets on reproduction of sows. *Agric. Res.* **49**, 943-953
- HUGHES, P.E. and COLE, D.J.A. (1975). Reproduction in the gilt. 1. Influence of age and weight at puberty on ovulation rate and embryo survival in the gilt. *Anim. Prod.* **21**, 183-189
- HUGHES, P.E. and COLE, D.J.A. (1976). Reproduction in the gilt. 2. Influence of gilt age at boar introduction on the attainment of puberty. *Anim. Prod.* **23**, 89-94
- HUGHES, P.E. and COLE, D.J.A. (1978). Reproduction in the gilt. 3. The effect of exogenous oestrogen on the attainment of puberty and subsequent reproductive performance. *Anim. Prod.* **27**, 11-20
- HUGHES, P.E. and VARLEY, M.A. (1980). *Reproduction in the Pig*. London, Butterworths
- JENSEN, A.H., GEHRING, M.M., BECKER, D.E. and HARMON, B.G. (1967). Effect of space allowance and tethering on pre- and post-pubertal behaviour of swine. *J. Anim. Sci.* **26**, 1467 (Abstract)
- JENSEN, A.H., YEN, J.T., GEHRING, M.M., BAKER, D.H., BECKER, D.E. and HARMON, B.G. (1970). Effects of space restriction and management on pre- and post-pubertal response of female swine. *J. Anim. Sci.* **31**, 745-750
- JOHNSON, H.H.K., MOUSTGAARD, J. and HOJGAARD-OLSEN, N. (1952). The significance of vitamin B₁₂ for the fertility of sows and gilts. *Anim. Breed Abstr.* **23**, 784
- KIRKWOOD, R.N. (1980). Puberty in the gilt. PhD Thesis. University of Leeds
- KIRKWOOD, R.N., FORBES, J.M. and HUGHES, P.E. (1981). Influence of boar contact on attainment of puberty in gilts after removal of the olfactory bulbs. *J. Reprod. Fert.* **61**, 193-196
- KIRKWOOD, R.N. and HUGHES, P.E. (1979). The influence of age at first boar contact on puberty attainment in the gilt. *Anim. Prod.* **29**, 231-238
- KIRKWOOD, R.N. and HUGHES, P.E. (1980a). A note on the efficacy of continuous vs limited boar exposure on puberty attainment in the gilt. *Anim. Prod.* **31**, 205-207
- KIRKWOOD, R.N. and HUGHES, P.E. (1980b). A note on the influence of 'boar effect' component stimuli on puberty attainment in the gilt. *Anim. Prod.* **31**, 209-211

- KIRKWOOD, R.N. and HUGHES, P.E. (1981). A note on the influence of boar age on its ability to advance puberty in gilts. *Anim. Prod.* **32**, 211–214
- KLOTCHKOV, D.V., KLOTCHKOVA, A. Ya., KIM, A.A. and BELYAEV, D.K. (1971). The influence of photoperiodic conditions on fertility in gilts. *10th Int. Cong. Anim. Prod., Paris*, pp. 1–8
- LARSSON, S., NILSSON, T. and OLSSON, B. (1966). Some aspects of the metabolic effect of amino acid supplementation of pig diets. *Acta vet. scand.* **7**, 47–53
- LODGE, G.A. and MACPHERSON, R.M. (1961). Level of feeding during early life and the subsequent reproductive performance of sows. *Anim. Prod.* **3**, 19–28
- LOVE, R.J. (1978). Definition of a seasonal infertility problem in pigs. *Vet. Rec.* **103**, 443–446
- MACPHERSON, R.M., HOVELL, F.D. De B. and JONES, A.S. (1977). Performance of sows first mated at puberty or second or third oestrus and carcass assessment of once bred gilts. *Anim. Prod.* **24**, 333–342
- MANDL, A.M. and ZUCKERMAN, S. (1952). Factors influencing the onset of puberty in albino rats. *J. Endocr.* **8**, 357–364
- MARTINAT, F., LEGAULT, C., DU MESNIL DU BUISSON, F., OLLIVIER, L. and SIGNORET, J.P. (1970). Retardation of puberty in the sow. In *Journées de la recherche porcine en France*, pp. 47–54. Paris, L'Institut Technique du Porc
- MAVROGENIS, A.P. and ROBISON, O.W. (1976). Factors affecting puberty in swine. *J. Anim. Sci.* **42**, 1251–1255
- MONTEIRO, L.S. and FALCONER, D.S. (1966). Compensatory growth and sexual maturity in mice. *Anim. Prod.* **8**, 179–192
- MORTON, J.R.C., DENENBERG, V.H. and ZARROW, M.X. (1963). Modification of sexual development through stimulation in infancy. *Endocrinology* **72**, 439–445
- NATHAN, S. and COLE, D.J.A. (1981). Boar contact during rearing and attainment of puberty in the gilt. *Anim. Prod.* **32**, 370 (Abstract)
- NTUNDE, B.N., HACKER, R.R. and KING, G.J. (1979). Influence of photoperiod on growth, puberty and plasma LH levels in gilts. *J. Anim. Sci.* **48**, 1401–1406
- PAREDIS, F. (1961). Investigations on fertility and artificial insemination in the pig. *Anim. Breed Abstr.* **30**, 2697
- PATERSON, A.M. and LINDSAY, D.R. (1980). Induction of puberty in gilts. 1. The effects of rearing conditions on reproductive performance and response to mature boars after early puberty. *Anim. Prod.* **31**, 291–297
- PAY, M.G. and DAVIES, T.E. (1973). Growth, food consumption and litter production of female pigs mated at puberty and low body weights. *Anim. Prod.* **17**, 85–91
- PHILLIPS, R.W. and ZELLER, J.H. (1943). Sexual development in small and large types of swine. *Anat. Rec.* **85**, 387–400
- PLUMLEE, M.D., THRASHER, D.M., BEESON, W.W., ANDREWS, F.N. and PARKER, H.E. (1956). The effects of manganese deficiency upon the growth, development and reproduction of swine. *J. Anim. Sci.* **15**, 352–367
- RAMIREZ, V.D. (1973). Endocrinology of puberty. In *Handbook of Physiology* (S.R. Geiger, Ed.), *Section 7, Endocrinology, Vol. II, Part 1*, pp. 1–28. Washington, D.C., American Physiological Society

- REDDY, V.B., LASLEY, J.F. and MAYER, D.T. (1958). Genetic aspects of reproduction in swine. *Res. Bull. Mo. agric. Exp. Stn.* No. 666
- REUTZEL, L.F. and SUMPTION, L.J. (1968). Genetic and phenotypic relationships involving age at puberty and growth rate in gilts. *J. Anim. Sci.* **27**, 27-30
- ROBERTSON, G.L., CASIDA, L.E., GRUMMER, R.H. and CHAPMAN, A.B. (1951a). Some feeding and management factors affecting age at puberty and related phenomena in Chester White and Poland China gilts. *J. Anim. Sci.* **10**, 841-866
- ROBERTSON, G.L., GRUMMER, R.H., CASIDA, L.E. and CHAPMAN, A.B. (1951b). Age at puberty and related phenomena in outbred Chester White and Poland China gilts. *J. Anim. Sci.* **10**, 647-656
- ROBISON, O.W. (1974). Effects of boar presence and group size on age at puberty in gilts. *J. Anim. Sci.* **39**, 224 (Abstract)
- SCANLON, P.F. and KRISHNAMURTHY, S. (1974). Puberty attainment in slaughter weight gilts in relation to month examined. *J. Anim. Sci.* **39**, 160 (Abstract)
- SCHEIMANN, C.A., ENGLAND, D.C. and KENNICK, W.H. (1976). Initiating estrus in pre-pubertal confinement gilts. *J. Anim. Sci.* **43**, 210 (Abstract)
- SCHMIDT, K. and BRETSCHNEIDER, W. (1954). The outward course of the sexual cycle in the sow. *Anim. Breed. Abstr.* **32**, 1046
- SELF, H.L., GRUMMER, R.H. and CASIDA, L.E. (1955). The effects of various sequences of full and limited feeding on the reproductive phenomena in Chester White and Poland China gilts. *J. Anim. Sci.* **14**, 573-592
- SHORT, R.E. (1963). Influence of heterosis and plane of nutrition on reproductive phenomena in gilts. M.S. Thesis. University of Nebraska
- SHORT, R.E., ZIMMERMAN, D.R. and SUMPTION, L.J. (1963). Heterotic influence on reproductive performance in swine. *J. Anim. Sci.* **22**, 868 (Abstract)
- SIGNORET, J.P. (1970). Reproductive behaviour of pigs. *J. Reprod. Fert. Suppl.* **11**, 105-117
- SIGNORET, J.P. (1972). The mating behaviour of the sow. In *Pig Production* (D.J.A. Cole, Ed.), pp. 295-314. London, Butterworths
- SIGNORET, J.P. (1980). Mating behaviour of the pig. In *Reviews in Rural Science, IV. Behaviour*, (M. Wodzicka-Tomazewska, T.N. Edey and J.J. Lynch, Eds.), pp. 75-78, Australia, University of New England
- SORENSEN, A.M., THOMAS, W.B. and GOSSETT, J.W. (1961). A further study on the influence of level of energy intake and season on reproductive performance of gilts. *J. Anim. Sci.* **20**, 347-359
- STICKNEY, K., FOXCROFT, G.R., GARSIDE, D.A. and MORTIMER, M.J. (1978). Aspects of oestrogen-induced puberty in the gilt. *Anim. Prod.* **26**, 388-389 (Abstract)
- SURMUHIN, A.F. and CEREMNYH, V.D. (1970). The effect of light on the development of the reproductive organs of gilts. *Anim. Breed. Abstr.* **39**, 3687
- SURMUHIN, A.F., CEREMNYH, V.D., TIMOFEEV, V.P. and POZNIKOVA, A.A. (1970). Development of gilts subjected to different light regimes. *Anim. Breed. Abstr.* **39**, 3602
- TASSELL, R. (1967). The effects of diet on reproduction in pigs, sheep and cattle. *Br. vet. J.* **123**, 170-176

- TEAGUE, H.S., ROLLER, W.L. and GRIFFO, A.P. Jr. (1968). Influence of high temperature and humidity on the reproductive performance of swine. *J. Anim. Sci.* **27**, 408-411
- THOMPSON, L.H. and SAVAGE, J.S. (1978). Age at puberty and ovulation rate in confinement as influenced by exposure to a boar. *J. Anim. Sci.* **47**, 1141-1144
- VANDENBERGH, J.G. (1969). Male odour accelerates female maturation in mice. *Endocrinology* **84**, 658-660
- WAHLSTROM, R.C. and LIBAL, G.W. (1977). Effect of dietary protein during growth and gestation on development and reproductive performance of gilts. *J. Anim. Sci.* **45**, 94-99
- WARNICK, A.C., WIGGINS, E.L., CASIDA, L.E., GRUMMER, R.H. and CHAPMAN, A.B. (1951). Variation in puberty phenomena in inbred gilts. *J. Anim. Sci.* **10**, 479-493
- WIGGINS, E.L., CASIDA, L.E. and GRUMMER, R.H. (1950). The effect of season of birth on sexual development in gilts. *J. Anim. Sci.* **9**, 277-280
- WISE, F.S. and ROBERTSON, G.L. (1953). Some effects of sexual age on reproductive performance in gilts. *J. Anim. Sci.* **12**, 957 (Abstract)
- WITZ, W.M. and BEESON, W.M. (1951). The physiological effects of a fat deficient diet on the pig. *J. Anim. Sci.* **10**, 957-959
- ZACHARIAS, L. and WURTMAN, R.J. (1964). Blindness: its relation to age of menarche. *Science* **144**, 1154-1155
- ZIMMERMAN, D.R., BOURN, P. and DONOVAN, D. (1976). Effect of "transport phenomenon" stimuli and boar exposure on puberty in gilts. *J. Anim. Sci.* **42**, 1362 (Abstract)
- ZIMMERMAN, D.R., CARLSON, R. and LANTZ, B. (1974). The influence of exposure to the boar and movement on pubertal development in the gilt. *J. Anim. Sci.* **39**, 230 (Abstract)
- ZIMMERMAN, D.R., CARLSON, R. and NIPPERT, L. (1969). Age at puberty in gilts as affected by daily heat checks with a boar. *J. Anim. Sci.* **29**, 203 (Abstract)
- ZIMMERMAN, D.R., SPIES, H.G., RIGOR, E.M., SELF H.L. and CASIDA, L.E. (1960). Effects of restricted feeding, crossbreeding and season of birth on age at puberty of swine. *J. Anim. Sci.* **19**, 687-694