HEAT STRESS AND REPRODUCTION IN PIGS: ITS ROLE IN SEASONAL INFERTILITY

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SUMMARY

A seasonal infertility in pig breeding herds is observed in Australia and overseas. It is characterised before mating by an increase in the incidence of anoestrus, delayed puberty in gilts and prolonged wean-to-mate intervals, and after mating by reduced conception rates, delayed returns to service, an increase in sows not-in-pig when due to farrow and possibly by increased abortions. Litter size is generally not affected. Because the infertility occurs during summer and increases in the above symptoms have been associated with elevated ambient temperatures, heat stress has been generally regarded as the immediate cause of the reduced fertility. .

Laboratory studies into heat stress of boars and sows have duplicated many of the field characteristics of seasonal infertility. However, some influences produced experimentally have not been observed under practical conditions.

Although heat stress appears at the moment to be the precipitating factor in a cumulative level of stress acting upon the sow, other influences may be involved in seasonal infertility. These include photo-period, nutrition, housing, social interactions, humidity and disease.

Various avenues for research are suggested.

INTRODUCTION

Australian interest in the influence of heat stress on reproduction in the boar and sow has been generated by the problem of so-called "summer infertility".

In the early 1970's Australian producers began to report that fewer sows than expected were farrowing in autumn/early winter. This decline in reproductive efficiency was detected as a result of the move to intensification and the consequent keeping of more accurate and informative records on the breeding herd and has since been documented (Stone 1977; Love 1978, 1981; Paterson et al. 1978; Williamson et al 1980). Similar seasonal fluctuations in reproductive efficiency have been reported overseas (New Zealand, Shearer and Adam 1973; Canada, Grandhi et al. 1977, Fahmy et al. 1979; U.S.A., Hurtgen and Leman 1980; Mexico, Aluja and Berruecos 1978; Norway, Benjaminsen and Karlberg 1981; England, Stork 1979; France, Corteel et al. 1964: Italy, Enne et al, 1979; Nigeria, Steinbach 1976).

The most obvious manifestation is now recognised as a reduction in the conception rate during summer months from a norm of 85 to 95% to as low as 50% (Anon. 1977; Baharin and Beilharz 1977; Stone 1977; Love 19.78, 1981; Paterson et al. 1978; Williamson et al. 1980; Johnston 1980; Hennessy 1983 - pers. comm.). Most studies have also shown there is variation in the onset, duration and severity of the problem between piggeries and within the same piggery from year to year (Cameron 1977;

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Love 1978; Hurtgen and Leman 1979; Stork 1979; Williamson et al. 1980). The infertility occurs in both extensive and intensive piggeries, but seems less severe under intensive management systems (Anon. 1977: Stone 1977).

Since the decline in reproductive efficiency occurred mainly during the summer'months, the stress imposed by high ambient temperatures was thought to be the immediate cause. The term "summer infertility" was . coined and research to date has been directed towards an understanding of the role of heat stress in the syndrome. However, these studies have indicated the possible involvement of other factors. Periods of infertility have been recorded in winter and autumn, as well as summer, also indicating that stressors other than heat were involved. This led Johnston (1980) to suggest the term "seasonal" rather than "summer" infertility, a suggestion supported by theresults of other studies (see below).

"Seasonal infertility" will be used in this paper which will examine the effects of high ambient temperature (heat stress) on the reproductive function of boars and sows, consider other factors which may contribute to the seasonal infertility and suggest areas for further investigation.

LABORATORY vs FIELD STUDIES

Our incomplete knowledge and understanding of the effects of high temperatures on boars and sows are based on observations made in field studies or from experiments carried out in controlled environment (hot) rooms. The temperature regimes imposed in laboratory studies of heat stress can, generally, in no way be considered representative of temperature conditions in the field. In many, the animals were exposed to constant high or low temperatures. While diurnal temperature variation was a feature of some laboratory studies, the change from warm to hot was in most cases rapid. It might thus be expected that the results of laboratory and field studies are not in total agreement.

Heat stress causes reproductive disturbances in three areas: the boar, the unmated sow and the mated sow.

EFFECT OF HEAT STRESS ON THE BOAR

Libido

Wrathall (1975 p.66) and Carr (1977) both assessed the effect of experimental heat stress on libido to be a direct and immediate reduction in sexual interest. However, this reaction is not universal. Although' a temperature of about 30°C appears to be critical (Winfield et al. 1981) libido was unaffected by even greater extremes of stress (Wettemann et al. 1977, 1979; Cameron and Blackshaw 1980; Stone 1982a).

Naturally occurring high temperatures also reduce libido (Wrathall 1975; Steinbach 1976) again particularly at temperatures above 30°C (Winfield et al. 1981). Steinbach (1976) speculated that this lack of libido may be related to reduced testosterone levels in the plasma of the heat-stressed boar. Stone (pers. comm. 1979) asserts that though testosterone levels are reduced, they are adequate to support normal male behaviour.

On the basis of these observations the advice of Winfield et al. (1981) is best followed: boars should be mated in well ventilated areas during the period of the day when temperatures are below 30°C.

Semen volume

Experimental exposure to heat stress does not generally reduce the volume of semen or gel (McNitt and First 1970; Wettemann et al. 1976, 1979; Cameron and Blackshaw 1980) though there are some contrary reports (Christensen et al. 1972; Stone 1982a). This maintenance of semen volume suggests that accessory gland function is not altered by high temperatures (Wettemann et al, 1976, 1979) even though heat stress can produce a marked change in testicular hormone production (Wettemann and Desjardins 1979; Stone 1982b).

The. influence of season on semen volume in the field is equivocal and has been variously reported as a decline (Lawrence et al. 1970; Knoll and Kastyak 1977; Peter et al. 1981), no effect (Serdyuk et al. 1977; Cameron 1980a; Egbunike and Dede 1980) or an increase (Cameron 1980a).

Low semen and gel volumes were concluded by Stone (1982a) to be of little consequence to fertility unless they reflect low plasma androgen levels which would then be related to changes in sperm maturation.

Semen quality

Heat stress causes semen quality to deteriorate. Concentration of sperm in the ejaculate, total sperm per ejaculate and daily sperm output may (McNitt and First 1970; Christensen et al. 1972; Wettemann et al. 1976, 1979) or may not (Cameron and Blackshaw 1980; Stone 1982a) decline but these authors and others (Mazzarri et al. 1968; Mazzarri 1971; Winfield et al. 1981; Einarsson and Larsson 1982) agree that motility of the sperm and percentage of morphologically normal sperm deteriorate dramatically.

The influence of natural heat stress on semen quality characters are very similar to those recorded under laboratory conditions (Lawrence et al. 1970; Wrathall 1975 p.66; Steinbach 1976; Knoll and Kastyak 1977; Serdyuk et al. 1977; Kopriva and Pikhart 1981; Peter et al. 1981), although Cameron (1980a) found there were no differences between winter and summer.

The duration of heat stress may be as important as the absolute temperature involved. The results of a number of hot room studies indicate that boars can tolerate temperatures as high as 40°C for up to four days before the cumulative effects of heat stress become detrimental (Winfield 1978; Cameron and Blackshaw 1980; Winfield et al. 1981; Einarsson and Larsson 1982).

Time course of heat stress on semen characteristics

The effects of heat stress on semen quality appear about two weeks after heat stress is first imposed, reach their maximum severity in 28-38 days and return to normal 5-8 weeks after the heat stress ceases (McNitt and First 1970; Christensen et al. 1972; Wettemann et al. 1976, 1979; Cameron and Blackshaw 1980; Winfield et al. 1981; Einarsson and Larsson 1982; Stone 1982a).

Effects of heat on spermatogenesis

The period between heat stress and the first appearance of depressed semen quality reflects the most advanced'sensitive cell type and the time for recovery indicates the extent of tissue damage (Stone 1979 - pers. comm.). It takes approximately 50 days to produce spermatozoa capable of fertilization (Stone 1982b).

The testes are extremely sensitive to heat stress under laboratory conditions. Direct application of heat to the scrotum for just three hours affected early spermatogenesis within 25 hours: the number of live spermatozoa in the ejaculate declined markedly two weeks after treatment (Mazzarri et al. 1968).

Since immature testicular spermatozoa take 9-14 days to pass through the epididymus and effects on semen quality were not observed until two weeks after the initiation of heat stress Wettemann et al. (1979) and Cameron and Blackshaw (1980) suggested that epididymal function in the boar is probably not easily affected by elevated temperatures i.e. that sperm in the epididymus are more resistant to heat stress than sperm in the testis. In contrast, Stone (1982b) concluded that mature cells are more sensitive based on observation of abnormal sperm in ejaculates after only one week of heating (Stone 1982a). However, he suggested this. greater sensitivity of epididymal cell types may also reflect the high sensitivity of the caput epididymus to heat stress (Stone 1981).

The effects of heat stress on spermatogenesis are further discussed by Wettemann et al. (1979), Wettemann and Desjardins (1979) and Cameron and Blackshaw (1980).

While not yet finally determined, the threshold ambient temperature at which sperm production is impaired appears to be about 32-35°C (Stone 1982a; Cameron and Blackshaw 1980). This agrees with the suggested critical temperature for sows (Paterson et al. 1978). Having observed differences in sperm production between the hottest and coolest months, Steinbach (1976) suggested that a rise of 1°C in the mean monthly temperature will cause a reduction of 4 x 10^9 sperm in each ejaculate about 56 days later.

F e r t i l i t y

Libido, semen quantity and quality combine to determine the fertility (impregnation or conception rate) and fecundity (litter size) of the boar. In laboratory studies, when heat-stressed boars were mated naturally or by artificial insemination to normal gilts the conception rate was reduced by up to 50% while litter size (embryo survival) and the proportion of normal embryos at 30 days of pregnancy may also be lowered (Christensen et al. 1972; Wettemann et al. 1976, 1979). Quality semen is necessary for high fertility (Wettemann et al. 1976) though it was later suggested that semen quality may not affect litter size when excess sperm from heated boars are deposited by natural mating (Wettemann et al. 1979). On the basis of semen characteristics Winfield et al. (1981) and Stone (1982a) considered boar fertility would have been reduced for a period of 4-5 weeks commencing 2-3 weeks after treatment.

These laboratory observations support those field reports of a boar contribution to lowered conception rates and smaller litters (Thibault et al. 1966; Signoret and du Mesnil du Buisson 1968; Entwistle et al.

1978; Wettemann et al.. 1978). However, Italian workers concluded the boar, at the most, played *only* a small part in the increased conception failure seen each summer (Enne et al. 1979). In Australian studies no evidence that impaired boar **fertility** contributed to seasonal infertility was found (Love 1978, 1981; Paterson et al. 1978), although Stone (1977) was unable to dismiss the possibility7

Effect of heat stress on testosterone production

Testosterone stimulates the development and maintenance of the accessory reproductive organs and the secondary sexual characteristics in the male. St is necessary'for the completion of spermatogenesis and stimulates the maturation and development of normal fertilizing ability of sperm.

Short term heat stress (35^{0}C for 24 hours) failed to depress plasma testosterone levels (Stone 1982b) but increasing the level and/or duration of heat stress can do so (Wettemann and Desjardins 1979; Einarsson and Larsson 1980; Stone 1982b). Steinbach (1976) proposed that the lower level of testosterone in the heat stressed **boar** may be responsible for the lower spermatogenic activity of the testes seen during summer (see above).

Adaptation to, and tolerance of, heat stress

Boars appear able to adapt to heat stress given sufficient time.

In prolonged heat stress the elevated rectal temperature and respiratory rate gradually decrease though they do not return to normal levels: semen characteristics respond similarly (Wettemann et al. 1976). Egbunike and Elemo (1978) have shown that European boars **can adapt** to a tropical climate and maintain normal semen production rates, while Cameron and Blackshaw (1980) reared animals at 30^{0}C and found that 35^{0}C or more was required to impair spermatogenesis.

Boars can be grouped according to their tolerance of high temperatures (Kopriva and Pikhart 1981) but such tolerance is highly individual (Wettemann et al. 1979; Cameron and Blackshaw 1980) and may have a genetic basis (Winfield et al. 1981). The **cyclical nature** of the heat stress imposed in some experiments may have allowed boars to tolerate higher temperatures for longer i.e. the cooler periods afforded relief (Winfield et al. 1981).

Areas for further investigation

(i) Fate of semen in heat-stressed sows Much is known of the effects of high ambient temperature on semen quality of heat stressed boars. Cameron (1983 - pers. comm.) has drawn attention to the fact that nothing is known of the fate of normal semen deposited in the reproductive tract of heat stressed sows in which body temperature is elevated. Would such elevated temperatures in the sow impair the fertilizing capacity of normal semen?

(ii) Reduced pheremone production Evidence is conflicting on whether the boar makes a direct contribution under field conditions to seasonal infertility via inadequate numbers of normal motile sperm in the ejaculate. A more subtle influence is suggested via a pheremonal effect on the sow and on the boar. The androstene steroids in the saliva of the boar stimulate and elicit the sexual response in sows but at the same time increases his own libido (Perry et al. 1980). If heat stress reduces the production of these steroids as it does of testosterone, then the success of mating may also be reduced, particularly if gilts or sows were at the same time showing sub-normal levels of oestrus behaviour. It has been clearly shown that high levels of courting behaviour (libido) in the boar have a beneficial effect on the success of mating (Hemsworth et al. 1978).

Conclusion

It is unclear from the information available whether the boar makes a direct contribution to seasonal infertility as a result of exposure to high temperatures. The most important effect of heating is a reduction in the number of normal motile sperm ejaculated and is seen about two weeks after heat stress (32-35^{0}C) of sufficient duration (about four days) is first imposed. As a result conception rates in females can be reduced.

EFFECT OF HEAT STRESS ON THE SOW

Since gilts and sows have a reproductive cycle, the effects of temperature stress on the female are'more complex. The overt responses are largely determined by the stage of the reproductive cycle at which the stress is imposed.

Before matina

(i) Anoestrus An increase in the incidence of anoestrus has been reported in both laboratory (Warnick et al. 1965; Edwards et al. 1968; Teague et al. 1968; D'Arce et al. 1970; Mercy and Godfrey 1980) and field studies (Steinbach 1972, 1976; Cameron 1977; Godfrey et al. 1983 - pers. comm.), though it is not an invariable effect of heat stress. Under practical conditions anoestrus was defined as the failure to observe oestrus within 30 days after weaning: up to 35% of sows weaned in the summer months have become anoestrus (Hurtgen 1976; Hurtgen and Leman 1979; Hurtgen et al. 1980a).

Somewhat related to anoestrus is the effect of high ambient temperatures on age and weight at puberty in gilts. Gilts reared during summer are commonly observed to be older and lighter at puberty than those which grow during the cooler seasons (Steinbach 1976; Anon. 1979; Cronin 1980; Anon. 1981; Christensen 1981).

(ii) Wean-to-mate interval Sows weaned during summer often exhibit a delay in returning to oestrus as distinct from anoestrus. Increased wean-to-mate intervals are described in various ways (Hurtgen 1976; Martinat-Botte et al. 1977; Fahmy et al. 1979; Hurtgen and Leman 1979, 1981a, b; Weckowicz 1979; Egbunike and Steinbach 1980; Hurtgen et al. 1980a; Benjaminsen and Karlberg 1981; Mišković et al. 1981) but all reflect the sow's reduced ability to resume ovarian activity in summer, (Benjaminsen and Karlberg 1981).

(iii) Cycle length Data on the influence of heat stress on the length of the oestrus cycle is conflicting and is available only from hot room experiments. Increases in cycle length of up to two days have followed exposure to high temperatures and may be associated with reduced feed intake during heating (Edwards et al. 1968; Teague et al. 1968; Pett 1983 - pers. comm.). Yet similar experimental regimes have caused no such changes (D'Arce et al. 1970; Mercy and Godfrey 1980; Godfrey et al. 1983 - pers. comm.) although an asynchrony between ovulation and oestrus was indicated by histological examination of the ovaries of heated gilts (D'Arce et al. 1970).

(iv) Duration and intensity of oestrus An experimental indication (Pett 1983 - pers. comm.) that the duration of oestrus may be reduced by heat stress is supported by observations from the field that the heat period was reduced by over half a day in summer (Steinbach 1976; Cleary 1983 - pers. comm.). Sexual interest of sows (Steinbach 1976) and intensity of oestrus (Cronin 1980) are also lower in summer, reductions which may be the direct result of a decline in oestrogen secretion (Steinbach 1976).

(v) Ovulation rate Ovulation rate may be slightly reduced in gilts which are heat stressed experimentally (Warnick et al. 1965; Edwards et al. 1968; Pan 1983 - pers. comm.), particular-temperature increases (Teague et al. 1968) and the period of exposure prior to ovulation lengthens (D'Arce et al. 1970). Stress prior to ovulation can not only block ovulation but also lead to cystic and inactive ovaries (Hennessy 1978). Other experiments' found'no effect on ovulation rate (Mercy and Godfrey 1980; Godfrey et al. 1983 - pers. comm.; Pett 1983 - pers. comm.) . Similarly summer temperatures did not directly affect ovulation rate (Steinbach 1976).

(vi) Conception rate and litter size Experimental heat stress prior to mating appears to have little effect on conception rate, or on the number (apart from the possibility of a reduced ovulation rate),survival and size of embryos in the subsequent pregnancy (Warnick et al. 1965; Edwards et al. 1968; Godfrey et al. 1983 - pers. comm.).

After mating

The susceptibility of mated gilts and sows to heat stress varies according to the stage of pregnancy.

(i) Early pregnancy Experimental heat stress during early pregnancy even for periods as short as l-2 days, can reduce fertilization of the ova (conception rate) (Mercy and Godfrey 1980), and increase embryonic mortality following fertilization. A series of studies (Jensen 1964; Warnick et al. 1965; Tompkins et al. 1967; Edwards et al. 1968; Omtvedt et al. 1971) revealed the relative importance of the pre-implantation (days 0-8 of pregnancy) and the implantation periods (days 9-16) in sensitivity to heat stress. A greater reduction in conception rate occurred when stress was applied on days 0-8 but the reduction in the number of viable embryos was greater when exposure was from days 9-16. This suggests the embryo is more vulnerable to heat. stress during implantation. The reduction in viable embryos represents only partial loss of the litter. Complete litter loss can also occur in a proportion of sows when heat stress is imposed during the first 14 days of gestation, with embryonic mortality in the surviving pregnancies being unaffected (Wildt et al. 1975). These complete litter losses may be seen as a delayed return to service (Godfrey et al. 1983 - pers. comm.).

A decline in the conception rate in summer is an almost universal observation in field studies of seasonal infertility (Corteel et al. 1964; Hurtgen 1976; Baharin and Beilharz 1977; Stone 1977; Grandhi et al. 1977; Paterson et al. 1978; Enne et al. 1979; Stork 1979; Cameron 1980b;

Egbunike and Steinbach 1980; Johnson 1980; Hurtgen and Leman 1981b). However, the decline in conception rate is only a generalised symptom which is due to delayed returns to service, in increase in sows found to be not-in-pig when due to farrow, and increased abortions (Corteel et al. 1964; Love 1978, 1981; Paterson et al. 1978; Stork 1979; Hurtgen et al. 1980a).

The major problem appears to be an increase in the proportion of sows returning to service between 25 and 33 days after mating (Love 1978; Paterson et al. 1978) and between.44 and 57 days (Love 1981). It appears that sows in this latter group experienced oestrus at 25-33 days but were either not detected or had a silent heat. The incidence of silent heats is higher in summer (Steinbach 1976; Williamson et al. 1980; Benjaminsen and Karlberg 1981; Christensen 1981).

Not-in-pig sows were also suggested to be sub-oestrus i.e. having silent heats, rather than anoestrus (non-cyclic) (Stork 1979). The increase in abortions seen by Stork (1979) are also reported to occur in Australia (Cutler 1983 - pers. comm.).

The cause of the delayed returns is unclear. Paterson et al. (1978) suggest that high temperatures around the time of mating alter ovarian function causing temporary infertility and an endocrine imbalance resulting in extended and irregular dioestrous intervals after the initial mating. Love (1978, 1981) proposed that early embryonic death due to high temperatures about seven days after mating was the immediate cause. Sows then return to oestrus 22-37 days after mating: some sows show heat and are mated while others go through a silent heat. In extreme cases sows may be not-in-pig when due to farrow. It was subsequently shown that at least 35% of sows with delayed returns had lost their litters and that in about 40% of delayed returns ovulation occurred but oestrus behaviour was not shown (Pan et al. 1983 - pers. comm.) thus supporting Love's suggestion. This suggested sequence of events recognises that embryonic death induced by experimental heat stress also occurs as a result of naturally high temperatures and that it is an all-or-nothing phenomenon; the sow either maintains the pregnancy and farrows a normal litter or loses the whole litter and returns to oestrus.

Apart from endocrine imbalance and embryonic mortality, large luteinized ovarian cysts and small ovarian cysts have been identified as part of the seasonal infertility syndrome (Williamson et al. 1980).

(ii) Mid-pregnancy From the end of the third week after mating to the end of the third month, gilts and sows are relatively resistant to heat stress under both experimental (Heitman et al. 1951; Tompkins et al. 1967; Edwards et al. 1968; Omtvedt et al. 1971) and field (Paterson et al. 1978) conditions. Heat stress at this time is likely to cause the death of the sow before causing death and abortion of the litter, possibly due to the combined influences of high ambient temperature and high metabolic heat production (a function of intra-uterine litter weight) affecting the heat balance of the sow (Steinbach 1976).

(iii) Late pregnancy and lactation Experimentally (Omtvedt et al. 1971) and naturally (Steinbach 1971) high temperatures during the last two weeks of pregnancy can cause death of the sow and increase stillbirths. These losses have not been recorded under practical conditions in Australia (Love 1978; Paterson et al. 1978).

Most studies show no effect of season on litter size as distinct from stillbirths (Steinbach 1971; Grandhi et al. 1977; Aluja and Berruecos 1978; Love 1978; Hurtgen and Leman 1979; Hurtgen et al. 1980b; Williamson et al. 1980) although birth weights of piglets from summer matings may be reduced (Steinbach 1971; Entwistle et al. 1976; Baharin and Beilharz 1977). A reduction in birth weight has also been induced experimentally (Omtvedt et al. 1971). Steinbach (1976) related a tendency to reduced litter weight gain in summer to the effects of high temperatures on the development of the mammary gland, on the endocrine glands important to milk synthesis and on lack of nutrients due to reduced feed intake.

Gilts vs sows

Gilts and first litter sows are more susceptible to seasonal reproductive problems than sows with two or more litters (Love 1978; Enne et al. 1979; Hurtgen et al. 1980a; Benjaminsen and Karlberg 1981; Hurtgen and Leman 1981a). Hurtgen and Leman (1980) observed that while fertility of gilts, primiparous and multiparous sows was uniformly lower in summer, delay in the onset of post-weaning oestrus in primiparous sows was exaggerated in hotter months, compared to multiparous sows.

Relation of ambient temperature with reproductive efficiency

It is difficult to define a critical temperature above which reproductive efficiency declines during the hotter months. Temperature data are presented in different ways: for Australia the graphs of Stone (1977) suggest an average maximum monthly temperature of 25-27°C, those of Love (1978) a mean monthly mid-afternoon wet-bulb temperature of 16-17°C, while an average weekly maximum of 32°C was indicated by Paterson et al. (1978). In Europe, a critical average monthly maximum of 20°C has been given (Stork 1979; Keindorf and Plescher 1981).

Seasonal infertility is recorded in countries with hot and with mild summers as illustrated by the temperatures above. This suggests that the effect of higher temperatures on reproductive performance is relative, or perhaps that that some other factor is also involved (see below).

In the Australian context, the threshold temperature-above which reproductive problems are likely to occur appears to be about 32°C.

Effect of heat stress on female reproductive hormones

Reproductive function in the female depends upon a series of hormones including follicle stimulating hormone, luteinising hormone, progesterone and oestrogen. The levels of these hormones vary with the stage of the oestrous cycle and the pregnancy status of the animal. While heat stress affects the sow at various stages of the reproductive cycle the hormonal mechanisms behind these responses are little understood (Wrathall 1975; Steinbach 1976; Kreider et al. 1978; Barb et al. 1979; Hurtgen and Leman 1979; Rampacek et al. 1979; Kattesh et al. 1980; Williamson et al. 1980; Benjaminsen and Karlberg 1981). It is uncertain whether the responses are due to a direct effect of heat stress on the sex hormones or whether these hormones are indirectly altered by changes in adrenocorticotrophic hormone (ACTH) and corticosteroid hormones induced by heat stress (Wrathall 1975).

Adaptation to, and tolerance of, high temperatures

Gilts and sows, like boars, are able to partially adjust to experimental high temperatures though the adaptation may be less pronounced during late pregnancy (Tompkins et al. 1967; Edwards et al. 1968; D'Arce et al. 1970; Omtvedt et al. 1971). There is some evidence that sows can adapt to natural high temperatures (Steinbach 1976) particularly if some relief is afforded by cooler nights (Cox et al. 1964). Within parity, the susceptibility (or tolerance) of individual sows to summer heat varies, as it does also from year to year for the one sow (Williamson et al. 1980). The reproductive function of the majority of sows is undisturbed.

Résumé

The basic symptoms of seasonal infertility are an increase in the incidence of anoestrus and a decline in the conception rate. This latter is manifest as an increase in the number of sows returning to service after a prolonged period and of sows not-in-pig when due to farrow. The cause of the prolonged returns (early embryonic loss or ovarian dysfunction) is uncertain. In general, once pregnancy is established it will be maintained without further loss unless the sow herself succumbs to heat stress in late pregnancy, although there is a low incidence of abortions.

While experimental heat stress may increase anoestrus, reduces conception rate and causes partial litter losses through early death of embryos, the greatest production losses may occur during late pregnancy. This is contrary to the field situation where the abnormally long return periods appear to cause the greatest loss in productivity.

INVOLVEMENT OF OTHER FACTORS IN SEASONAL INFERTILITY

It was first suggested by Greer (1980) and Williamson et al. (1980), and is now generally agreed, that the manifestations of seasonal infertility are not solely due to heat stress. Rather, it is due to the sum of a number of cumulative stressors acting on the animal, many of which are present all year. The additional stress imposed by high summer temperatures are thought to result in the stress threshold-being exceeded and the characteristics of seasonal infertility are then observed. Other stressors which may be involved include social interactions (including group size) management influences, housing, humidity, nutrition and disease.

Nutrition

Nutritional status may be an important factor in seasonal infertility, representing an indirect effect of high temperatures. Feed intake is generally reduced by high temperatures, a problem which may be exacerbated by the normally lower feed intakes and lower quality diets given to Australian sows. The benefits of higher than normal intakes during lactation and after weaning on reproductive efficiency have been demonstrated (King 1982).

Reduced feed intake may in part be responsible for the greater susceptibility of young sows to seasonal infertility (Love 1978). Certainly, increasing the nutrient density of the diet to compensate for reduced feed intake has markedly improved the performance of sows

(Steinbach 1976; Cox et al. 1983) and growing pigs (Farrell 1981) exposed to high temperatures.

Group size

Studies on the influence of penning system (group vs individual) on reproduction in the weaned sow are contradictory. None-the-less, while Hurtgen and Leman (1980) found farrowing rate was lower for group-housed sows, the depression in farrowing rate during summer was also greater. This reduction may be due to the additional stress of bullying by other sows.

Photoperiod

The association of summer temperatures with seasonal infertility might simply be co-incidental to changes in daylength during spring and autumn. Seasonal infertility may be a relic of the annual photoperiodic rhythm which occurs in the pigs' wild ancestors. The wild pig issexually inactive in summer and autumn: this inactivity is thought to be mediated by changes in daylength (Stork 1979). A number of studies suggest photoperiod may be a significant factor in seasonal infertility (Egbunike and Steinbach 1980; Hurtgen et al. 1980a, Benjaminsen and Karlberg 1981) although Christensen (1981) concluded otherwise.

Another indication that high temperatures may not be solely responsible for seasonal 'infertility is the failure of evaporative cooling to exert a beneficial effect (Hurtgen et al. 1980a; Hurtgen and Leman 1980). Equally, however, these results also suggest that if heat stress is involved in seasonal infertility, then present cooling systems do not effectively minimize heat stress factors.

Areas for further investigation

(i) The role of nutrition and photoperiod Nutritional strategies have potential as a simple means of alleviating seasonal infertility. Increasing digestible energy intake during periods of high temperature appears to be the most promising approach but the involvement of other nutrients (e.g. protein, vitamins) should not be ignored. Likewise the involvement of photoperiod requires clarification: both duration and intensity of light may be involved.

(ii) Hormonal responses to stress The manifestations of seasonal (stress) infertility are now fairly well established but our understanding of the mechanisms behind these effects is not clear. The responses to stress of both the adreno-corticoid (stress) hormones and the sex hormones (in both the boar and the sow) at all stages of the reproductive cycle require definition. It should then be possible to understand how the effects of stress are exerted within the animal. From this might follow the formulation of strategies to obviate hormonal responses to stress and maintain hormonal patterns within normal bounds.

(iii) Identification of susceptible animals A large proportion of gilts/sows are unaffected by seasonal infertility though this resistance can vary from year to year. Greer suggested that if susceptible animals could be identified then during the period of seasonal infertility they could be husbanded so the total level of stress to which they were subjected was kept below the critical threshold. Pan (1983 - pers. comm.) has proposed an alternative approach - identify stress susceptible animals and include in the breeding programme active selection for stress tolerance. This strategy has been successful with mice (Pennycuik 1979).

COST TO THE AUSTRALIAN PIG INDUSTRY

An estimate of the financial loss caused by seasonal infertility can be made from the data provided by Stone (1977). For the Australian herd of 342,550 sows (at 31 March, 1981 - A.B.S. 1983) the value of the lost production of 222,700 pigs per year at February, 1983 pig and feed prices was $6.63m nett.

This is an under-estimate: the national reduction in reproductivity may be greater than found by Stone (1977) and the margin between costs and returns in February, 1983 was low.

CONCLUSION

Seasonal infertility is normally seen during the summer/early autumn months. The characteristics of seasonal infertility have been established, but the causes are not clear. Many of the characteristics have been reproduced by experimental heat stress. Relationships between high summer temperatures and lowered reproductive efficiency have also been demonstrated. These two factors, however, cannot be taken as an indication that seasonal infertility is due solely to heat stress. The influence of heat stress may be indirect, being mediated by reduced nutrient intake. Or its involvement may be co-incidental to an effect of photoperiod: conversely, if photoperiod is a factor in seasonal infertility it may act by pre-disposing sows to the effects of heat stress i.e. the stressors which trigger the syndrome may be acting on an animal with the remnant of a propensity towards a reproductive "rest-period". The cost of the syndrome to the Australian pig industry justifies further research.

ACKNOWLEDGEMENTS

I thank my colleagues for allowing me to mention the results of their unpublished work and Drs. W.L. Bryden and Y.S. Pan for their comments.

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