

Management of boars for efficient semen production

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Consistent production of large quantities of fertile semen is a primary concern of boar management programmes. Common visual tests such as motility are poor indicators of the fertilizing capacity of an ejaculate. Research studies have demonstrated that, in general, if motility is 60% or greater, there are no relationships among the percentage of motile spermatozoa, *in vitro* sperm penetration rates, farrowing rates and litter size. Biological and environmental factors that influence the production of total numbers of spermatozoa are either inhibitory or stimulatory. Chronic undernutrition and heat stress inhibit spermatogenesis, while photoperiod and genetic factors are stimulatory. A consistent stimulatory effect of photoperiod does not appear to occur under all environmental conditions. In contrast, selection for increased testis size consistently results in greater sperm production. In addition, libido is decreased by heat stress and undernutrition. However, failure to allow boars to interact socially with other pigs during pubertal development appears to be the most damaging factor. Effective boar management programmes must minimize the occurrence of factors that adversely affect spermatogenesis and simultaneously accentuate those with a stimulatory role.

Introduction

Each time a mating occurs, the boar and sow are generally viewed as contributing equally towards its outcome. Fertilization requires placement of adequate numbers of fertile spermatozoa in the female reproductive tract before ovulation which is closely linked to reproductive processes and behaviour in boars. Establishment of pregnancy involves maintenance of a uterine environment conducive for embryonic and fetal development which is predominantly a biological function of sows. However, when the entire breeding herd is considered, a single boar has a significantly greater impact on efficiency and productivity than an individual sow. This is because a female normally produces two litters per year, whereas a male can sire from 50 to 3000 depending on the type of mating system that is used. Consequently, management strategies for boars tend to influence herd productivity in an exponential fashion and are a major component of reproductive efficiency of swine operations.

Regardless of whether matings are natural or artificial, production of fertile spermatozoa is an absolute requirement for boars and the measure by which their reproductive merit should be evaluated. Therefore, the primary intent of this review is to examine recent developments in terms of our current understanding of biological and environmental factors that influence qualitative and quantitative aspects of sperm production in boars. In addition to spermatogenesis, mating behaviour of boars also has important ramifications with regard to the efficient production of semen especially in breeding programmes using artificial insemination. Consequently, a secondary objective is to consider strategies that have been implemented to enhance the sex drive of boars. The end result should be a summary of relevant reproductive and management data from which informed decisions can be made with regard to managing semen production in boars.

Semen Production

Consistent production of large numbers of fertile spermatozoa is the ultimate goal of a successful boar management programme. As a result, qualitative and quantitative aspects of semen production have been the primary focus of research for improving boar fertility. For the purposes of this review, quality will refer to fertility, defined as the ability of semen to produce live pigs, and quantity will be defined as the number of spermatozoa produced. It is important to note that there is not an obligatory association between these two aspects of semen production. Thus, each will be considered separately.

Production of fertile semen

The ability to assess the fertility of semen is a necessary prerequisite for studying the effects of various management strategies designed to improve its quality. In both the scientific and commercial sectors of the swine industry, the most commonly used tests for evaluating sperm quality involve visual estimations of the percentage of motile or morphologically normal spermatozoa (Colenbrander and Kemp, 1990; Woelders, 1991). Furthermore, a common assumption is that ejaculates with a high percentage of motile or morphologically normal sperm cells are of higher quality and more fertile than those with low estimates of the same parameters. In fact, a common practice within commercial boar studs is to adjust the total number of spermatozoa in insemination doses based on sperm motility, or morphology or both factors (Colenbrander *et al.*, 1993). While it is true that, during fertilization, pig spermatozoa rely on their forward motion to move through the cumulus layers and penetrate the zona pellucida (Polge, 1978), the value of using the motility of a raw ejaculate as an indication of its ability to fertilize eggs upon insemination is less clear (See Holt and Medrano, this supplement). In other species, the percentage of motile sperm cells is generally considered to be a poor measure of semen fertility (Linford *et al.*, 1976; Amann, 1988).

Results from a recent study (Flowers and Turner, *in press*) that examined the relationship between motility and fertility are presented in Table 1. In this experiment, spermatozoa were obtained once a week from 12 mature boars for 26 weeks. Evaluations for motility were conducted on each ejaculate. A portion of each collection was processed for *in vitro* fertilization, while the remainder was extended and used to inseminate at least five sows. Semen characteristics were divided into ten groups, for example 90 to 100%, 80 to 89%, and treated as an independent variable. Special precautions were taken to ensure that all insemination doses administered to an individual sow during oestrus and the corresponding subsample used *in vitro* were from the same motility classification. Consequently, the experimental design provided both *in vitro* and *in vivo* estimates of fertility for ejaculates exhibiting a wide range of semen motility.

These data provide several important observations concerning the use of the percentage of motile spermatozoa as an estimate of semen fertility in swine. First, motility, at best, can be used to establish the lower limit of acceptability for semen use, but is of little analytical value for ejaculates above this value. This is evident in that sperm penetration rates, farrowing rates and number of pigs born alive were not different among ejaculates estimated to contain more than 60% motile spermatozoa. In contrast, reproductive performance was reduced in sows inseminated with semen the motility of which was less than 60%. Second, there appear to be individual boars that deviate from this general relationship between motility and fertility. When motility groups were considered in conjunction with individual boar effects, a significant interaction was present. This interaction was attributed to boars whose fertility tended to be low when semen parameters were high or vice versa (Table 2). Finally, inclusion of additional visual criteria such as morphology and acrosome integrity do not improve the predictive value of motility. Adjustments for morphology and acrosome integrity within each motility group did not alter the relationship between the percentage of motile spermatozoa and fertility estimates (data not shown). In summary, it appears that use of the percentage of motile spermatozoa is a qualitative rather than a quantitative measure of semen fertility.

This conclusion should not be surprising. In addition to the mechanical requirements associated with egg penetration, spermatozoa must also undergo biochemical, metabolic and molecular

Table 1. Relationships among motility, sperm penetration rates, farrowing rates and number of pigs born alive for boar semen

Motility ^a (%)	Sperm penetration rate ^b (%)	Farrowing rate ^c (%)	Number born alive
94.7	89.5 ^v (58)	86.9 ^v (460)	10.6 ^v
82.3	81.7 ^{vw} (55)	87.1 ^v (330)	10.5 ^v
76.1	84.3 ^{vw} (50)	84.5 ^v (300)	10.5 ^v
66.2	74.7 ^w (44)	86.1 ^v (264)	10.1 ^v
52.4	55.5 ^x (40)	72.4 ^w (201)	9.2 ^w
44.2	34.7 ^y (28)	72.3 ^w (168)	9.2 ^w
32.6	21.3 ^z (17)	51.7 ^x (85)	7.8 ^x
SEM ^p	4.8	5.8	0.3

^aMotility is expressed as the average number of motile spermatozoa within the following classes: > 90; 80–89; 70–79; 60–69; 50–59; 40–49; and 30–39.

^bSperm penetration rate is defined as the percentage of eggs that were fertilized. Numbers in parentheses represent the number of ejaculates within a motility category.

^cNumbers in parentheses represent the number of sows inseminated with semen within a motility category.

^dStandard error of the mean.

^v^w^x^y^z Means within the same column with different superscripts are significantly different ($P < 0.05$).

changes before they acquire fertilizational competence. A variety of different tests based on one or more of these events has been or is in the process of being developed (Table 3). For some of these tests there are estimates of their relationship to sperm fertility. The most promising of these attempt to quantify specific aspects of sperm binding to egg membranes or structural changes within sperm membranes or DNA. Obviously, the ideal fertility test for efficient production of semen needs to be proactive, accurate, quick and economical. While many of these new tests appear to fulfil the first two requirements, most require extended analytical periods or sophisticated equipment. As a result, their acceptability and use within the commercial sector, at the present time, remains to be determined.

In addition to spermatozoa, there is an increasing abundance of evidence that indicates that other components in semen participate in physiological events associated with fertilization (Claus, 1990; Flowers and Esbenshade, 1993; Waberski *et al.*, 1995; Waberski, this supplement). Consequently, it is reasonable to speculate that male fertility may be related, in part, to concentrations of these compounds normally present in semen. At the present time, there is little direct evidence for this speculation in swine. However, consideration of the results from several related experiments provide indirect support for this contention.

In a recent study, DNA fingerprinting techniques were used to determine the paternity of piglets within a litter when several boars were used for breeding (Flowers *et al.*, 1996). The conclusions were that a single boar sired the majority of pigs within a litter (> 80%) and that this boar was usually the one used for mating 12 or 24 h after the first detected oestrus. This was expected because previous studies have suggested that the mating that occurs closest to ovulation yields most of the piglets within a litter (Vesseur *et al.*, 1996) and, in this particular herd, the average oestrus-to-ovulation interval was determined by ultrasonography to be 32.6 ± 4.5 h. However, there was one boar that consistently sired the majority of pigs within a litter when he mated sows at 0 and 12, but not 24, h after the onset of oestrus. These data are presented in Table 4 and this boar was referred to as being

Table 2. Relationships among semen motility, sperm penetration rates, farrowing rates and number of pigs born alive for four individual boars

Boar number	Motility ^a (%)	Sperm penetration rate ^b (%)	Farrowing rate ^c (%)	Number of pigs born alive
1	87.3±5.3 ^x (26)	84.6±4.8 ^x	83.2±6.3 ^x (147)	10.9±0.3 ^x
2	78.3±6.1 ^x (26)	62.3±5.1 ^y	67.3±5.8 ^y (133)	9.5±0.4 ^y
3	55.3±5.7 ^y (26)	81.4±6.7 ^x	84.1±6.1 ^x (130)	10.7±0.3 ^x
4	51.3±4.1 ^y (26)	52.3±5.4 ^y	70.3±4.8 ^y	8.7±0.3 ^y

^aMotility is the average percentage of motile spermatozoa. Numbers in parentheses indicate the number of ejaculates that were evaluated.

^bSperm penetration rate is the average percentage of eggs that were fertilized.

^cNumbers in parentheses indicate the number of sows that were mated per boar.

^{x,y}Means within the same column with different superscripts are significantly different ($P < 0.05$).

dominant because if he was used for the first or second mating, then he sired the majority of the litter. One of the explanations for this observation was that, for whatever reason, spermatozoa from the dominant boar were retained longer in the female reproductive tract than were those of other males used in the study (designated as non-dominant). Variation among boars in the retention time of their spermatozoa in the female reproductive tract has been described by Mburu *et al.* (1996) and, in this particular case, was confirmed by subsequent studies as numbers of oviductal spermatozoa from the dominant boar at 24 h after mating were five times higher than those from non-dominant males (W. L. Flowers, unpublished). An equally feasible explanation that was not explored was that the dominant boar induced an earlier ovulation compared with non-dominant boars. Both retention of spermatozoa in the female reproductive tract and advancement of ovulation have been attributed to seminal plasma (Claus, 1990; Waberski *et al.*, 1995).

Another study was initiated in which heterogeneous inseminations were made by mixing the sperm-rich and seminal plasma fractions of the dominant boar with those of a non-dominant male to determine whether this advantage in sperm retention was a function of spermatozoa or seminal plasma (W. L. Flowers, D. G. McLaren and K. Siggins, unpublished). An outline of the experimental design is shown (Fig. 1). The various combinations of spermatozoa and seminal plasma were used for matings at first detected oestrus, whereas additional boars were used for matings 12 and 24 h later. Paternity results from these mating treatments are shown in Table 5.

These results indicate that at least part of the dominance effect resides in the seminal plasma. This is evident by the fact that the proportion of piglets sired by the dominant boar was lower when his spermatozoa were mixed with seminal plasma from a non-dominant male, whereas the converse was true with the reciprocal combination, non-dominant semen with dominant seminal plasma. With regards to semen fertility, the relevant finding in this study was that the paternity pattern for piglets was altered by the removal and addition of seminal plasma to spermatozoa. Thus, the relative importance of seminal plasma and its composition deserves consideration when attempting to evaluate the fertility of pig semen. Further credence for this statement is provided by recent studies with cattle. In dairy bulls, the presence of four seminal plasma proteins has been shown to be highly correlated with fertility (Killian *et al.*, 1993), and there is a strong relationship between calving rates and concentrations of heparin-binding proteins in semen of beef bulls (Bellin *et al.*, 1994).

In summary, to produce fertile pig semen, it is necessary to evaluate its fertility accurately. At the present time, most of the visual criteria used to assess semen quality are, at best, crude indicators of its fertilizing properties. Consequently, as new tests with greater accuracy are developed, it will be important to use these for evaluation of semen not only on commercial farms, but also in the

Table 3. Summary of various measurements used to estimate fertilizing ability of boar spermatozoa

Measurement	Rationale	References
Percoll gradients	Velocity of spermatozoa is positively correlated with fertility. Spermatozoa with increased velocities can be separated via Percoll gradients	Grant <i>et al.</i> , 1994
Fluorescent stains	Some fluorescent stains (Hoechst 33258) enter sperm cell if membrane is damaged and stain only dead cells. Others (SYBR-14) enter spermatozoa with a membrane potential and stain only live cells	Johnson <i>et al.</i> , 1996
Sperm chromatin structure	When subjected to acidic conditions and stained with metachromatic dye acridine orange, double-stranded DNA give a green fluorescence, while single-stranded DNA (damaged) give a red fluorescence. Ratio of green to red spermatozoa is related to fertility	Evenson <i>et al.</i> , 1994
Sperm plasma membrane protein profile	Plasma membrane proteins were separated and quantified. Three proteins were positively correlated with sperm binding to egg membranes ($r=0.38$ to 0.53). Two proteins were negatively correlated with sperm binding ($r=-0.42$ and -0.37)	Ash <i>et al.</i> , 1994
Oocyte membrane binding assay	Fertile spermatozoa bind to egg membranes. Correlation between egg binding and fertility <i>in vivo</i> from heterospermic inseminations was 0.80	Berger <i>et al.</i> , 1996
Hemizona binding assay	Oocytes are bisected and the number of spermatozoa from different boars binding to each half of the zona pellucida are counted. Within a hemizona pair, increased binding equates to increased fertility	Fazeli <i>et al.</i> , 1995

research community as strategies for enhancing male fertility are investigated. Moreover, the composition of seminal plasma may also need to be included in future assessments of semen fertility.

Production of total number of spermatozoa

In general, management programmes designed to optimize production of the total number of spermatozoa can be divided into two general categories: (i) prevention of detrimental situations and (ii) enhancement of stimulatory influences. In essence, techniques in the first group can be thought of as removal of situations that reduce spermatogenesis, while those in the latter classification are attempts to enhance male gamete formation. Although most of the techniques discussed are dependent upon the age of the boar, there are a few instances where prepubertal males appear to respond in a different way from mature males. When appropriate, these situations will be acknowledged and discussed.

Table 4. Paternity distribution (% \pm SEM) of pigs from sows mated to three different boars during oestrus

Variable ^a	First sire ^b	Second sire ^b	Third sire ^b
Litters in which the dominant boar was the first sire (10)	89.3 \pm 7.5 ^x	4.5 \pm 1.2 ^x	6.2 \pm 1.3 ^x
Litters in which the dominant boar was the second sire (10)	7.7 \pm 4.3 ^y	88.2 \pm 8.6 ^y	4.3 \pm 1.2 ^x
Litters in which the dominant boar was the third sire (10)	25.4 \pm 7.5 ^z	35.7 \pm 8.2 ^z	38.1 \pm 9.1 ^z
Litters in which non-dominant boars were used as sires (70)	25.7 \pm 3.3 ^z	41.5 \pm 3.7 ^z	32.8 \pm 4.5 ^z

^aNumbers in parentheses indicate number of litters that were evaluated.

^bFirst, second and third sire refer to boars that inseminated sows at 0, 12 and 24 h after the onset of oestrus, respectively.

^{x,y,z}Means with different superscripts within the same column are significantly different ($P < 0.05$).

Prevention of detrimental situations. Nutritional influences on sperm production in mature boars have been reviewed by Colenbrander and Kemp (1990) and Kemp and Verstegen (1991). The general consensus from studies in this area is that prolonged periods of undernutrition reduce the total number of spermatozoa produced. Specifically, the magnitude of protein and energy restrictions reported varied from 25–60% and 15–67%, respectively, and the restriction period had to be at least 6–8 weeks before significant differences were observed. The negative effect of undernutrition on spermatogenesis is more pronounced when protein rather than energy is restricted. In fact, Louis and coworkers (1994a) did not observe a reduction in sperm output in boars on a restricted energy diet. However, when dietary levels of only protein or both protein and energy were lowered, the total numbers of spermatozoa were reduced by 18% and 27%, respectively. Similar studies conducted in prepubertal boars revealed that moderate restrictions in energy and protein during sexual maturation did not affect spermatogenesis (Hacker *et al.*, 1994).

Several different groups have attempted to estimate protein and energy requirements for male reproduction (Kemp *et al.*, 1991; Close and Roberts, 1993). For mature boars (226 kg), 37 MJ of metabolizable energy and 230 g of crude protein per day appear to be adequate for meeting maintenance, libido and spermatogenic requirements. It is important to note that maintenance requirements for boars are influenced by a variety of environmental factors including health status, ambient temperature and frequency of use. Thus, it is probable that maintenance needs for boars differ among farms. As a result, variability in studies investigating the effect of energy and protein manipulations on reproductive function in boars should be expected.

Perhaps a more relevant point of discussion concerning boar nutrition is the early identification of suboptimal nutritional regimens. Because spermatogenesis requires between 39 and 50 days in boars (Swierstra, 1968), numbers and morphology of spermatozoa would not be expected to reflect nutritional deficiencies immediately. Consequently, a problem could remain undetected for several months. In studies that used chronic restriction regimens, aberrant mating behaviour consistently preceded measurable changes in ejaculate characteristics (Louis *et al.*, 1994a, b). These included extended recognition times, reduced durations of ejaculation and increased frequencies of mating refusals. On the basis of these observations, changes in normal mating behaviour may have potential for use in diagnosing marginal protein and energy deficiencies in boars.

In contrast to the effects of nutrition, exposure to high ambient temperatures has immediate, severe and consistent effects on spermatogenesis (Christenson *et al.*, 1972; Wettemann and Bazer, 1985). These include ejaculation of a large proportion of spermatozoa with morphological abnormalities, fewer

Table 5. Paternity distribution (%+SEM) of pigs from sows mated with various combinations of seminal plasma and spermatozoa from dominant and non-dominant boars at the onset of oestrus

Treatment*	First mating ^b	Second mating ^c	Third mating ^c
Dominant spermatozoa + dominant seminal plasma (10)	80.3±6.1 ^x	8.1±3.2 ^x	11.6±3.9 ^x
Dominant spermatozoa + non-dominant seminal plasma (10)	62.2±8.3 ^y	17.4±6.9 ^x	20.4±5.1 ^x
Non-dominant spermatozoa + dominant seminal plasma (10)	48.8±9.1 ^y	30.1±5.4 ^y	18.7±6.2 ^x
Non-dominant spermatozoa + non-dominant seminal plasma (10)	22.4±8.3 ^z	44.1±5.9 ^z	33.5±6.1 ^y

*Numbers in parentheses indicate number of litters that were evaluated.

^bFirst mating refers to combinations of seminal plasma and spermatozoa from dominant and non-dominant boars that were administered at the onset of oestrus.

^cSecond and third matings were administered at 12 and 24 h after the onset of oestrus, respectively, by non-dominant boars not used for the first mating.

^{x-z}Means with different superscripts within the same column are significantly different ($P < 0.05$).

spermatozoa and reduced fertility. The minimum exposure time and critical air temperature above which sperm production is impaired have been reported to be 30°C (Stone, 1982) and 72 h (McNitt and First, 1970), respectively. However, most of the studies conducted to date have used longer periods of exposure (1–4 weeks) and higher temperatures (33–37°C).

Obviously, an important aspect of efficient semen production is to prevent boars from being exposed to acute periods of heat stress. However, few studies have examined alterations in sperm output from boars exposed for extended periods to temperatures in the upper range of their thermal comfort zone, 26–29°C. Chronic exposure to temperatures within this range probably occurs routinely during the summer months in mechanically ventilated facilities located in temperate and semi-tropical climates. Field data from seven commercial boar studs in southeastern North Carolina from June through September is shown in Fig. 2. Each stud houses an average of 200 boars and has a weekly production goal of 2000 insemination doses. The average weekly high temperature in these facilities never increased above 29°C during the recording period. However, a significant increase in the number of ejaculates that were rejected due to poor quality and a corresponding decrease in the number of insemination doses per ejaculate were observed. It is interesting to note that the downward trend in the number of doses per ejaculate began 5 to 6 weeks after the weekly high temperatures stabilized at 27.5°C. In acute studies, a lag period of about 2 weeks is commonly observed between the initiation of heat stress and the first indications of abnormal sperm production (Wettemann *et al.*, 1979). It is possible that these data provide indirect evidence that boars may also be sensitive to chronic periods of moderately high temperatures not normally associated with heat stress conditions. The longer interval between the temperature increase and the first signs of abnormal sperm production may reflect a gradual reduction in the ability of boars to dissipate heat or subtle adjustments in energy partitioning to compensate for the increased demands for maintaining thermal neutrality over an extended period. Regardless of the mechanism, these field data indicate that the idea of chronic heat stress resulting from long periods of exposure to moderately high temperatures merits further investigation.

Enhancement of stimulatory influences. From a physiological perspective, an increase in the total number of spermatozoa produced can be accomplished in one of two ways: either by increasing the number of type A spermatogonia that initiate mitosis at a given time or by increasing the frequency

		Spermatozoa	
Seminal plasma	Dominant	Non-dominant	
	+	+	
	Dominant	Dominant	
	<hr/>		
Dominant	Non-dominant		
+	+		
Non-dominant	Non-dominant		

Fig. 1. Experimental treatments consisting of combinations of spermatozoa and seminal plasma. Sperm rich fractions of semen were collected separately from seminal plasma of dominant and non-dominant boars and recombined in a factorial arrangement of treatments as indicated (sperm origin plus seminal plasma origin).

at which this occurs. Both processes are regulated by complex endocrine and paracrine interactions. As a result, most of the management strategies that have attempted to increase sperm production are believed to work through these regulatory pathways.

The effect of photoperiod on sperm production in boars still awaits resolution. Studies investigating the influence of changes in photoperiod on sperm production are equivocal. Mazzari *et al.* (1968) reported that mature boars exposed to long daylengths exhibited a reduction in total numbers of spermatozoa. In contrast, other studies have reported increased spermatozoa output by increasing light when natural daylength is decreasing or by decreasing light when the natural daylength is increasing (Claus and Weiler, 1985). Brandt and Diekman (1985) did not observe any effects of supplemental lighting on spermatogenesis or concentrations of LH and testosterone. A similar situation is found for the influence of photoperiod on sperm production in prepubertal boars. Additional lighting may hasten the onset of mature testicular function (Hoagland and Diekman, 1982), but does not appear to yield consistent effects on cellular and endocrine aspects of spermatogenesis (Brandt and Diekman, 1985; Minton and Wettemann, 1987).

Thus, it is difficult to formulate definitive recommendations regarding the optimal lighting regimen for spermatogenesis. In addition, failure to measure changes in endocrine activity associated with photoperiodic responses suggests that while in unique situations the light:dark ratio may temporarily influence spermatogenesis, it is probably not a major avenue through which sperm output can be manipulated with consistent results. This statement is supported by the observation that in most males, including wild boars, in which spermatogenesis is linked to photoperiod, there is a corresponding change in the secretion of gonadotrophins and testosterone (Mauget, 1982).

In contrast to the influence of photoperiod, there appears to be a high positive correlation between testis size and sperm production in both prepubertal and mature boars (Rathje *et al.*, 1995). Boars selected for testis size produced 14.6×10^9 more spermatozoa than did randomly selected control males (Huang and Johnson, 1996). On the basis of the industry standard of $3-4 \times 10^9$ spermatozoa per insemination, these values would translate into an additional four to five doses per week. Furthermore, repeatabilities for sperm production traits in this study were reported to be between 0.26 and 0.40 (Huang and Johnson, 1996). Collectively, these data indicate that selection for increased testis size can be used to enhance the reproductive capacity of boars.

As stated earlier, management strategies that enhance sperm production, including selection for increased testicular size probably have a strong endocrine component. This is because most major testicular functions such as establishment of normal populations of Sertoli and Leydig cells and regulation of the timing and frequency of spermatogenic waves are controlled primarily by testosterone, gonadotrophins and growth hormone (Sharpe, 1995). Consequently, hormonal manipulation may offer potential for increasing sperm production. However, for this approach to be practical, identification of critical periods during which brief periods of administration would have long-lasting effects on

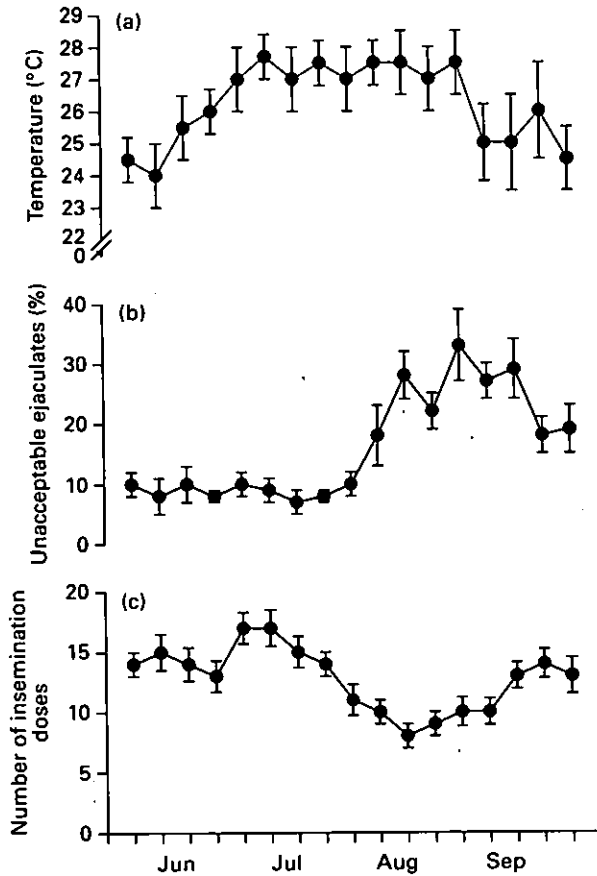


Fig. 2. Mean weekly high ambient temperature (a), percentage of ejaculates rejected for further processing (b) and average number of insemination doses per ejaculate (c) for commercial boar studs in North Carolina between June and September.

spermatogenesis is necessary. At the present time, several studies indicate that this may be possible. Swanlund *et al.* (1995) administered FSH or growth hormone to boars between 8 and 40 days of age. Growth hormone promoted tubular and Sertoli cell maturation, whereas FSH increased the number of Sertoli cells. In another study, administration of a reversible goitrogen, 6-propyl-2-thiouracil, for the first 8, 16 or 24 days after birth increased testis size and daily sperm production in adult rats (Cooke *et al.*, 1992). Obviously, considerably more research is needed to determine whether sperm production in boars can be manipulated effectively via hormonal regimens. However, it is important to remember that the use of exogenous gonadotrophins and prostaglandins at specific times during the production cycle has proved to be beneficial for enhancing reproductive efficiency in female swine.

Libido and Mating Behaviour

In boar management programmes, maintenance of high levels of libido probably deserves equal consideration as increasing sperm output. It could be argued that production of large amounts of fertile semen is of limited value if the desire to mate is not present. Unfortunately, our current understanding of factors affecting the sex drive of boars is more anecdotal than scientific. This may be

Table 6. Summary of management situations that influence libido and mating behaviour in boars

Situation	Age	Effect	Reference
Protein restriction	Mature (> 1 year)	Increased time to initiate ejaculation Decreased duration of ejaculation	Louis <i>et al.</i> , 1994a,b
<i>Ad libitum</i> feeding	Prepubertal (between 1 and 8 months of age)	Decreased chomping and salivation	Hacker <i>et al.</i> , 1994
Individual housing	Prepubertal (between 1 and 8 months of age)	Increased recognition time Increased incorrect mounts Decreased mating scores	Hemsworth <i>et al.</i> , 1977 Hacker <i>et al.</i> , 1994
High temperatures	Mature (> 1 year)	Decreased mounting attempts Decreased duration of ejaculation	Christenson <i>et al.</i> , 1972 Claus and Weiler, 1985
Decreased light when natural photoperiod is increasing	Mature (> 1 year)	Decreased reaction time	Claus and Weiler, 1985
Supplemental light	Prepubertal (between 15 and 32 weeks of age)	Increased libido scores	Berger <i>et al.</i> , 1980; Hoagland and Diekman, 1982

because behavioural responses are often more variable and less repeatable than physiological responses.

The results of several studies that have examined the influence of various aspects of the production environment of sexual behaviour in boars are summarized (Table 6). Collectively, these data indicate that isolation during pubertal development, chronic nutritional restriction and exposure to high ambient temperatures reduce libido or the performance of male mating behaviours. The effect of isolation during pubertal development appears to be related to the lack of experience in practising or participating in mounting behaviours during adolescence (Hemsworth *et al.*, 1977), while nutritional and environmental effects are related, at least in part, to a reduction in the endocrine activity of the hypothalamo-hypophyseal-testis axis (Wetteman and Desjardins, 1979; Louis *et al.*, 1994b). It is interesting to note that most of the detrimental influences outlined in Table 6 are chronic as opposed to acute deficiencies in the production environment.

Reports of strategies with acute effects on libido in boars are scarce. Intuitively, administration of testosterone would seem to be a logical approach. Although testosterone does produce short-term improvements in sex drive and mounting activity, it also results in a suppression in spermatogenesis if used for extended periods owing to its negative effect on LH secretion (Bishop *et al.*, 1992). Prostaglandins are involved in a variety of male sexual behaviours (Miesel and Sacks, 1994) and, thus, are commonly administered in an attempt to stimulate sexual interest and mounting behaviour in boars. Definitive studies are still needed to establish the effectiveness of this practice and any repercussions it may have on sperm production.

Conclusion

Most visual tests commonly used to evaluate semen quality in boars are poor indicators of fertility. As a result, our current understanding of the manner in which nutrition, environment and other management parameters affect sperm fertility from studies that have used these tests may not be as accurate as once believed. Consequently, as tests more closely linked to the fertilization process are developed, it may be necessary to revisit some of these areas of research. In addition, it appears that most of the situations that are detrimental to sperm production and male sexual behaviour, with the obvious exception of exposure to acute heat stress conditions, result from chronic or long-term inadequacies in the production environment. Given the relatively short period during which boars are normally used within operations for breeding, 7 months to 1.5 years, management of boars during pubertal development should be given as much, if not more, consideration as the manner in which they are handled as adults.

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