

Lactational Estrus in Sows, a Way to Increase the Number of Farrowings Per Sow Per Year

¹M. Alonso-Spilsbury, ²L. Mayagoitia, ³M.E. Trujillo, ¹R. Ramírez-Necoechea and ¹D. Mota-Rojas,

¹Ethology Laboratory, Metropolitan Autonomous University-Xochimilco (UAM-X),
Calzada del Hueso 1100, Colonia Villa Quietud, Mexico, D. F. 04960, Mexico

²Ethology Department, National Psiquiatric Institute (INP), Camino de Xochimilco 101,
Colonia San Lorenzo Huipulco, Tlalpan, Mexico, D. F. 14370, Mexico

³Veterinary Medicine Faculty (FMVZ), National Autonomous University of Mexico (UNAM),
Ciudad Universitaria, Circuito exterior, Coyoacán, Mexico D. F. 14370, Mexico

Abstract: During lactation the sow generally remains anestrus. However, lactational estrus and ovulation sometimes occurs under unusual circumstances. Practical outcomes of lactational estrus are reducing the interval between weaning and estrus and therefore the non-productive days in the herd. Although various techniques to induce lactational estrus have been performed through natural management of the animals or the use of exogenous hormones during lactation, induction of estrus during lactation has not been recommended for commercial use. The objective of this study was to review and analyze the basic lactating sow physiology and the different methodologies to induce lactational ovulation, in order to improve her reproductive and productive performance, as a possible alternative to the early weaning system, especially in those cases where lactation length is determined by welfare constraints.

Key words: Lactational estrus, endocrinology, sows, ovulation

Introduction

A common practice in swine production is to increase the number of litters per sow per year by reducing the intervals between farrowings with the use of an early weaning system (Dial *et al.*, 1995 and King *et al.*, 1998). This practice allows increasing productivity while reducing the lactation length; piglet health and growth rate is improved, preventing vertical transmission of disease from the sow to the piglets (Dritz *et al.*, 1994). From an economic perspective shorter lactation lengths have cost savings and make better use of farrowing rooms. Unfortunately, these potential benefits are sometimes nullified by a reduction in the subsequent reproductive performance of the sow (Xue *et al.*, 1993). Alternatively, to this technique, breeding sows during the lactation period increase their productivity too. This manipulation proves sometimes to be successful, it will enhance the development of the litter without affecting the reproductive cycle of the sow and the piglets will continue nursing even though the dam is pregnant. Therefore, reducing the reproductive cycle and obtaining a greater number of litters per sow per year (Kirkwood and Thacker, 1998). The interval between farrowings may be reduced if the sows are able to conceive during estrus, which would at the same time allow for a decrease in non-productive days in the herd.

Studies published in the 1950's, indicate that behavioural estrus occurs in 50 to 99% of the pigs at or just after farrowing (Warnick *et al.*, 1950; Baker *et al.*, 1953; Self and Grummer, 1958). This estrus is anovulatory, except in unusual circumstances such as the death of the litter or the removal of the piglets at birth (Warnick *et al.*, 1950). Under natural conditions, the sows that have farrowed show estrus between the fifth and tenth day post partum. This heat is anovulatory and can occur in 80 to 99% of the sows (Burger, 1952). Also, under natural conditions the sows show a tendency to reduce nursing initiation, especially after the 10th week post partum (Alonso-Spilsbury and Mayagoitia, 1998) and all throughout the 14th or 17th week (Jensen, 1986). This reduction in the frequency of lactation allows a positive feedback of GnRH, eliciting FSH and LH release, thus allowing the sow to manifest signs of estrus. Lactational estrus without ovulation could be due to an insufficiency of gonadotrophins or specifically to a failure in the release of FSH and synthesis of LH (Cole *et al.*, 1972; Guthrie *et al.*, 1978). Induced pregnancy during lactation has a moderate success only after the third week of lactation (Crighton, 1970b; Newton *et al.*, 1987a and Varley and Foxcroft, 1990); however, detection of estrus during lactation is difficult and the subsequent litter size has been reduced (Varley and Foxcroft, 1990). Although complete involution of the uterus does not occur until about 3 weeks into lactation, it would appear that most of the important changes have taken place by day 7 of lactation and there seems little reason why the uterus should not function again normally by 2-3 weeks post partum (Graves *et al.*, 1967). The latter point is extremely pertinent to the success or failure of early weaning (EW) systems (Hughes and Varley, 1980), since incomplete uterine involution is generally accepted as a contributing factor to the reduced embryo survival of EW sows.

According to Hays *et al.* (1978) and Marsteller *et al.* (1997), short lactation lengths do not seem to reduce the

number of eggs shed (ovulation rate) or the percentage of those eggs that are fertilized, but the percentage of embryos that survive is substantially reduced by day 25 to 30 post-mating. The suckling stimulus is almost certainly involved in the control of uterine involution as suckled sows show a faster rate of involution than sows which have had their litters removed very early in lactation (Graves *et al.*, 1967).

Varley and Atkinson (1985) have shown that although a majority of sows remain anestrus or did not show estrus on day 30 post partum (according to the levels of progesterone in plasma), 28% of the pigs had silent heats on 13.8 days average after parturition, while in a further 38% estrus and ovulation occurred 12.1 days post partum. Kemp (1998) indicates six factors that increase the incidence of lactational estrus: frequent boar contact, group housing systems, low milk production (low number of piglets), high food intake, split weaning and interrupted suckling and advanced parity of the sow. Besides these, some other factors influencing the occurrence of lactational estrus have been identified: sow weight and weight change during lactation (Bryant *et al.*, 1983b) and litter size (Rowlinson and Bryant, 1981). Also, induction of estrus and ovulation in a lactating sow can be achieved using exogenous hormones (Crighton, 1970a and b; Rowlinson *et al.*, 1974 and Petchey and Jolly, 1979).

Various authors (Petchey and English, 1980; Rowlinson and Bryant, 1981, 1982b; Bryant *et al.*, 1983ab and Hultén, 1995a) suggest that the presence of estrus during lactation is due to lactations longer than 45 days, grouping lactating sows and the presence of a boar.

The present review will address first the basic lactating sow physiology, so a better understanding of the different methodologies to induce lactational ovulation is achieved in the second part.

Factors Affecting the Presence of Lactational Estrus: The factors that affect the occurrence of lactational estrus are the suckling stimulus that reduces the secretion of gonadotrophins by the hypothalamus (Armstrong *et al.*, 1988a) and the metabolic state of the lactating sow. Suckling stimuli does not allow for post partum ovulation, inhibits the release of GnRH and promotes the release of prolactin, oxytocin and opioids. All of these hormones play an important role in the modulation of estrus.

Stimulation During Suckling

Gonadotrophin Release Factor (GnRH): The inhibition of GnRH release during lactation suppresses release of FSH and LH, eliciting lack of estrus (Britt *et al.*, 1985). If suppression of GnRH production is a cause of lactational anestrus, administration of GnRH at an appropriate dose and frequency might overcome lactational anestrus. Furthermore, pulsatile administration of GnRH induces follicular growth, estrus and ovulation in lactating sows (Cox and Britt, 1982). Suckling frequency and social interaction between the sow and her piglets decrease when sows are group-housed (Stolba *et al.*, 1990).

Luteinizing Hormone (LH): Once the sow has farrowed and initiated lactation, the ovaries become inactive for an approximate period of 10 days. Although small follicles might begin to develop after this period, rarely do they become a Graaf follicle (Britt *et al.*, 1985).

During lactation the LH pulses decrease in frequency, gaining amplitude which affects the positive feedback of FSH and makes the ovaries inactive. The suppression of the pulsatile LH release during lactation is an important reason why a sow normally remains anestrus during lactation (De Rensis *et al.*, 1996; Kemp, 1998). In fact, separation of the sow and piglets for periods of 4 h or more per day has been shown to increase basal LH concentrations (Armstrong *et al.*, 1988a). In the absence of lactation during this post partum period, the elevated levels of LH can promote highly estrogenic follicles showing cysts (Foxcroft *et al.*, 1992). Furthermore, it has been reported that although some zero-weaned sows show within 2 weeks an ovulatory heat of normal duration, other animals show a high incidence of cystic ovaries, prolonged non-ovulatory estrus and an increasing interval from farrowing to conception (Varley and Foxcroft, 1990). The number of sows that develop follicular cysts also increases following short lactation lengths (Self and Grummer, 1958 and Svajgr *et al.*, 1974). In other words zero-weaned or very early weaned sows that develop cystic follicles are characterized by one or more of the following: 1) prolonged and unpredictable return to estrus, 2) constant estrus 3) prolonged anestrus and 4) irregular returns (Britt, 1996).

There is accumulating evidence that the suckling induced suppression of LH release may be mediated by opioid peptides (Malven, 1986; Armstrong *et al.*, 1988ab and Kemp, 1998).

Prolactin: The ovary is one of the target tissues for prolactin (Dusza and Tilton, 1990). The levels of prolactin in plasma reach its maximum peak 8 to 12 hours after farrowing (Castrén *et al.*, 1993) and then decrease during lactation (Algers *et al.*, 1991). During lactation, suckling of piglets results in an elevation of prolactin levels about 10-15 min after initial nuzzling and teat message and returns to basal levels about 30-40 min after suckling (Kendall *et al.*, 1983). A gradual decrease in prolactin levels is seen during the course of lactation, apparently as a result of a gradual decrease in suckling frequency (Holmes *et al.*, 1988). After six hours of reaching its basal levels, a mechanism of positive GnRH feedback is established (Loseth and Crabo, 1994).

Prolactin levels are elevated during suckling stimulus and estrus cycle (Stevenson *et al.*, 1981; Edwards and

Foxcroft, 1983). A rapid decline in this hormone is seen after weaning (Foxcroft *et al.*, 1987) in most zero-weaned animals (De Rensis *et al.*, 1993), or when piglets are separated from sows during partial weaning (Stevenson *et al.*, 1981 and Shaw, 1984).

The prolactin released by the nursing sow can inhibit the ovarian function in an indirect way by influencing the release of LH pulses and inhibition of the ovarian estradiol synthesis (Dusza and Tilton, 1990).

If the sow is to enter lactational estrus, the levels of prolactin should descend so that GnRH will stimulate release of LH and FSH. Prolactin is also indispensable in the induction and the maintenance of LH receptors (Holt *et al.*, 1976). The LH and the FSH are slowly secreted during prolonged lactations and only in these cases the sows are capable of exhibiting fertile estrus (Hughes and Varley, 1980).

Prolactin not only plays a role in steroidogenesis, it enhances lipoprotein concentrations by maintaining the membrane receptors for the high-density lipoproteins (HDL), that are precursors of luteal steroidogenesis (Murphy and Rajkumar, 1985). Prolactin also stimulates progesterone secretion in luteal cells during the early stages of pig luteal function. As such, the luteotropic function of this hormone during lactation and the estrus cycle is still controversial.

Endogenous Opioids: Suckling stimuli induces the release of endogenous opioids in the sows' brain (Varley and Foxcroft, 1990 and Rushen *et al.*, 1993) and inhibits the release of GnRH and LH concurrently. There has been recent interest in the role of opioids and their antagonists in the control of ovulation. Experiments performed on lactating sows demonstrate that when given naloxone (an opioid antagonist), an increase in LH release and pulsatility occurred (Barb *et al.*, 1986 and Mattioli *et al.*, 1986) while concentrations of peripheral prolactin decreased (Armstrong *et al.*, 1988a; De Rensis *et al.*, 1993 and 1996). Moreover, Armstrong *et al.* (1988b) indicated that morphine –agonist endogenous opioid- diminished the secretion of LH after removal of the litter. Inhibition effect of prolactin also occurred, a suggestion that two different opioid receptors exist (De Rensis *et al.*, 1996).

Metabolic State of the Sow: Recently, several researchers have suggested that changes in reproductive hormone release in response to dietary manipulation are mediated through a blood metabolite, metabolic hormone, or a combination of metabolites and hormones, rather than through direct effects of body fat or protein reserves.

As it has been stated, suckling stimuli causes a neuroendocrine reaction involving prolactin and oxytocin, both of which contribute to the metabolic changes that occur during lactation and promote the use of protein and energy reserves (carbohydrates and fat) in milk synthesis (Einarsson and Rojittikhun, 1993).

If food intake is low, energy and protein requirements do not allow milk production. Therefore, the sow enters a negative energy deficit that produces the catabolic process where her energy deposits will be used. This catabolic state is evaluated according to the metabolites and metabolic hormone concentration, which means that if there is an increase of urea, fatty acids and creatinin, instead of milk production the protein and energy reserves are being used by the sow (Quesnel and Prunier, 1995).

It is important to recognize that the sow's milk production increases during the first 3 to 4 weeks of lactation and the effect of the catabolic state in the sow in regards to the metabolites and metabolic hormones is more pronounced when lactation is in progress and the reserves of energy are depleted (Kemp, 1998).

If food intake is low during lactation, it will provoke an inhibition of LH pulses before ovulation. Consequently luteinization of the corpora lutea and a decrease of progesterone levels in plasma during early pregnancy jeopardize embryo survival. Moreover, hyponutrition during lactation, besides from its effects on the sow as well as on the nursing piglets, also affects the reproductive performance of the female in the subsequent reproductive cycle. The quantity of food given to lactating sows is not the only important factor; individual differences have been found in the regulation of the metabolic energy level during the lactation period of sows that are well nourished (Rojittikhun *et al.*, 1992).

A protein and energy restriction during lactation produces a suppression of LH release in the pituitary gland, caused in turn by a decrease of the release GnRH in a lactating sow with a large litter or in primiparous sows. On the contrary the administration of glucose during lactation increases the levels of insulin in plasma, but does not have positive results on the LH levels (Tokach *et al.*, 1992).

Pettigrew and Tokach (1993) showed that insulin receptors are found in the brain and pituitary gland and that *in vitro* insulin enhances the release of FSH and LH. Whereas Cox *et al.* (1987) demonstrated that insulin injection in the cerebro-ventricular area elicited LH production, indicating there is a direct effect of insulin on the hypothalamic/pituitary axis that increases the ovulation rates.

It has been established that occurrence of lactational estrus is positively related to weight gain (or less weight loss) and negatively related to litter size during the group housing period (Petchey and Jolly, 1979; Rowlinson and Bryant, 1982b). Moreover, *ad libitum* feeding decreases weight loss during lactation in group-housed sows and seems to increase the occurrence of lactational estrus (Rowlinson and Bryant, 1982ab).

Follicular Development: There is extensive *in vitro* evidence of glucose, insulin and various growth factors (like IGFs and TGFs) effects on follicular development (Cox *et al.*, 1987; see Cosgrove and Foxcroft, 1996, for a review). Meurer *et al.* (1991) proved that the presence of follicular atresia in diabetic sows is due to the lack of insulin, as administration of insulin facilitates ovulation in sows. According to Poretsky and Kalin (1987), insulin might stimulate the granulosa cells to form LH receptors and produce estrogen. Also, overfeeding induced increases in follicular aromatase activity and/or follicular development, that has been associated with a marked increase in insulin status (Cosgrove *et al.*, 1992). Previous studies done by Cox *et al.* (1987) showed that the ovulation rate was higher when administering insulin alone or combined with an increase caloric intake during the follicular growth in primiparous pigs. These different experiments demonstrate a strong link between insulin and follicular development, but it is important to understand that there are metabolic and growth factors that are involved, though their participation is unknown and is still under study (Kemp, 1998).

Methods Used to Induce Lactational Estrus: Diverse techniques to induce lactational estrus have been used such as: partial litter weaning (Burger, 1952; Smith, 1961; Duggan *et al.*, 1982; Varley and Foxcroft, 1990; Loseth and Crabo, 1994 and Mota *et al.*, 2002); pheromonal stimuli from a mature boar (Smith, 1961; Cole *et al.*, 1972; Henderson and Hughes 1984; Stevenson and Davis, 1984; Newton *et al.*, 1987b and Costa and Varley, 1995); grouping lactating sows (Rowlinson *et al.*, 1982ab; Rowlinson *et al.*, 1974; Petchey and Jolly, 1979; Duggan *et al.*, 1982; Henderson and Stolba, 1989 and Hultén *et al.*, 1995 ab); communal lactating of sows in outdoor systems (Jensen and Stangel, 1992 and Alonso-Spilsbury *et al.*, 1998); gonadotrophin treatments (Crichton, 1970 ab; Hausler *et al.*, 1980; Kirkwood and Thacker, 1998); estrogen treatments (Cox *et al.*, 1988); administration of GnRH (Guthrie *et al.*, 1978 and Cox and Britt, 1982) and application of peptide opioids (Barb *et al.*, 1986 and Armstrong *et al.*, 1998 ab).

Most of the researchers have used one or a combination of more than one method with various degrees of success in inducing lactational estrus. Due to the limited success of these techniques, none of them have been commercially adopted.

Grouping Sows and Litters Plus Contact with the Boar: The use of natural methods, avoiding the use of exogenous hormones, consists of grouping lactating sows and their litters while allowing contact with a boar (Stolba *et al.*, 1990; Vesseur *et al.*, 1995 and Wechsler, 1995, 1996). This method has been very successful on occasions (Rowlinson *et al.*, 1975; Stolba *et al.*, 1990; Alonso-Spilsbury *et al.*, 1998), but in others there is no apparent effect on the manifestation of lactational estrus (*e.g.* Petchey *et al.*, 1978), or it is disadvantageous delaying the breeding period of group-housed sows (Hultén *et al.*, 1995ab).

Boar presence generally causes a high estrus frequency (Rowlinson *et al.*, 1975; Rowlinson and Bryant, 1981) and if sows are mated the conception rate is often high, indicating normal ovulations. Rowlinson and Bryant (1982b) found that grouping sows and their litters on the 10th day of lactation and introducing the boar 24 hours later, resulted in 100% of the sows showing signs of estrus on approximately the 34th post partum day and the subsequent litter size was about 11 piglets. Petchey and Jolly (1979) found that of the 49% of the sows kept with their litters that presented lactational estrus in the study, 78% conceived without problems. Yet sows breed at the early stages of lactation farrowed lighter piglets compared with sows that were mated during advanced lactation, indicating that lactational estrus is associated with decreased milk production. Concerning the above, there are works reporting contradictory results. Crichton (1970b) found that the piglets that had been weaned from pregnant-lactating sows weighed 0.45 kg more than the controls. On the other hand, Rowlinson and Bryant (1982a) did not find any differences. This finding could well be related to other variables. Although there is no work showing that lactational estrus produces lighter litter weights, it is known that group-housed sows during lactation interrupt the nursing process, by favoring cross-suckling (Algers, 1991) and making it easier for dominant piglets to increase their milk intake, while weaker piglets reduce their own (Hultén *et al.*, 1995ab). The apparent disadvantage of is that cross-suckling gives some sows the opportunity to abandon their piglets, leaving nursing to the other sows of the group (Bøe, 1994). Alternatively some piglets might abandon their mothers and nurse with other sows, causing their weight after weaning to be heterogenous and that some sows may lose weight during that process (Henderson and Stolba, 1989).

The grouping system, -often used in Swedish farms- presents advantages in reproductive terms, it has been demonstrated that not all sows show the same behavior; the multiparous present atrophy of the teats before weaning, due to the lack of stimulation of being suckled, which does not occur with the primiparous (Hultén *et al.*, 1995b). This might be due to the decrease in contact between the sow and her piglets, which seems mainly to occur in older sows, whereas younger sows seem to maintain in close relationship with their offspring (Hultén *et al.*, 1995b). This clearly illustrates that the housing systems will have to be used according to the category of the sows that will be managed in it.

Stolba (1981 and 1982) has demonstrated that lactational estrus can be consistently induced in sows housed in enriched environment family pens. The Pig Family Pen system, originally designed by Stolba (1981), consists in

managing small groups of related pigs housed in specifically designed pens, having an enriched environment, provided with areas of activity and straw bedding. Four sows are housed with their litters, allowing a boar to stimulate them 20 days after farrowing. Favorable results include the conception of sows 38 ± 12 days after birth, a reproductive cycle of 150 ± 15 days and 2.4 farrowings per sow per year (Stolba, 1984). Even allowing prolonged lactation, the sows weaned the litters naturally between the 12th and 14th weeks post partum (Moser, 1989).

The Pig Family Pen was put into practice by Wechsler (1996), finding that the sows presented lactational estrus before piglets were 7 weeks old, this happened in 53.8% of the cycles, the sows reared 21.4 piglets a year, showing that this system has advantages comparable to the intensive production.

Hultén *et al.* (1995a) studies comparing systems, group-housing versus single penned sows, found that 65% of the sows showing lactational ovulation were mated within 10 days after weaning in the group-housing system. Moreover, he found that parity number seemed to strongly influence the occurrence of lactational ovulation. None of their conventionally housed sows ovulated, supporting previous reports concluding that ovulations are rare among singly housed lactating sows (Burger, 1952 and Kunavongkrit *et al.*, 1985).

Partial Weaning of the Litter: Lactational estrus induction through partial weaning of the litter was recommended by Marshall and Hammond since 1937. Afterwards, Smith (1961), induced estrus by separating for 12 hours the litters on the 21, 31 and 35 days of lactation, observing that primiparous sows needed at least 14 days of separation to induce estrus and second parity sows needed only 5-6 days of separation when the treatment had begun on the 21st day of lactation. Eight hours separation on a daily basis after the 21st day of lactation did not produce estrus in any of the sows until the 8th week of lactation.

At present, the techniques used to induce lactational estrus or reduce the interval of weaning-estrus are a reduction of the litter size many days before weaning the sow (Stevenson and Britt, 1980; Stevenson and Davis, 1984), or fractionated weaning, in which the heavier piglets in a litter are weaned, followed by the weaning of the lighter pigs a few days later (Cox *et al.*, 1983; Henderson and Hughes, 1984; Kunavongkrit *et al.*, 1985; Riley *et al.*, 1985 and Matte *et al.*, 1992). Generally these treatments reduce the weaning-estrus interval without undesired effects in the subsequent fertility rate or litter size. Regarding this statement, it is important to note that Vasseur (1997) found better rates of fertility in sows that had been subjected to split weaning in a previous lactation.

Considering that separating the litter from the mother for a period of 4 hours or more a day, elicits LH increase (Booman and van der Wiel, 1980; Newton *et al.*, 1987ab; Armstrong *et al.*, 1988a), one should study the feasibility of using this procedure without compromising the health and growth of the piglets. For example, 10 years of experience managing grouped sows separated from their litters 4 hours daily –divided in two hours in the morning and two hours in the afternoon– during the first 15 days post partum and stimulated from day 17 to 20 by a group of boars showed very good results: 2.59 farrowings per sow per year, conception rates of 89%, a total of 9.48 born alive piglets, a total of 24.27 piglets per sow per year; 21% of the sows presented estrus before the 25 days post partum and the periods between farrowings and conception was 23.63 days (Anon, 1984). Although this experience has never been repeated.

Loeth and Crabo (1994) performed experiments with two groups of females; the control group remained with its litters 24 hours a day, in the experimental group the litter was removed 8 hours a day, during this time the sows had contact with a boar to evaluate the presence of estrus. In the experimental group the levels of prolactin decreased to 50% in one hour, 20% more in three hours and returned to the basal levels six hours after litter removal. Moreover, 4 of the 6 females were mated on days 5 and 6 after initiating the separation.

More recently, Mota *et al.* (2002) demonstrated that both partial withdrawn of the litter and boar stimulus induced lactational estrus without negative effects. Sows in this study significantly shortened their reproductive cycle; 100% of the sows showed estrus on day 11 post partum, they did not show non-productive days and furthermore, their litter size was increased in their subsequent farrowing.

From these studies we can conclude that the percentage of sows exhibiting an induced estrus in lactation varies considerably, from 45.5% (Burger, 1952), to 100% (Rowlison and Bryant, 1981; and Mota *et al.*, 2002). Differences in the mode of estrus induction are probably the cause of variation between experiments. Burger (1952) relied solely on the technique of removing the litters from the dams for 12 hours daily in lactation, whereas Rowlison and Bryant (1981) grouped sows and litters at day 20 of lactation and introduced a boar to the whole group a day later. On the other hand, Mota *et al.* (2002), removed the litters from the dam on day 11 for 4 hours and introduced the boar at the same time. A factor in common within these three experiments is that sows were housed either in pens or grouped and lactation was longer than 21 days.

Communal Lactation in Outdoor Systems: Preliminary works (Bryant *et al.*, 1983a) have shown that the intervals between sucklings are much more prolonged when housing sows in groups or when they are kept separated from their litters, this probably enhances estrus during lactation (Castrén *et al.*, 1989; Henderson and Stolba, 1989; Stolba *et al.*, 1990).

Results from Jensen and Stangel (1992), showed that European domestic sows maintained in temperate forests show lactational estrus. Similarly, preliminary results obtained in Mexico (Alonso-Spilsbury *et al.*, 1998), demonstrated that the Mexican hairless sow kept in agro-forestry conditions, allowed prolonged lactations of more than 10 weeks, also presented lactational estrus and 30% of the herd became pregnant while lactating. Both research groups coincide in that only one third of the animals had a shorter reproductive cycle of 140 days, achieving 2.8 farrowings per sow per year. What is not clear from both studies is whether the stimuli was caused by the boar, as it was in permanent contact with the sows, or if it was due to separation of the sows from their litters, which prolonged the intervals between sucklings (Alonso-Spilsbury and Mayagoitia, 1998). Most surely the results can be attributed to both stimuli (Crighton, 1970a; Stolba *et al.*, 1990 and Vesseur *et al.*, 1995), plus the administration of food *ad libitum* (Rowlinson *et al.*, 1975; Rowlinson and Bryant, 1982ab).

Use of Release Factors: Cox and Britt (1982) administered to lactating sows on the 24th day of lactation, GnRH pulsés at doses of 2.5 ig every 2 hours for 7 days. Fifty percent of the treated sows showed estrus 4 days after beginning the treatment and got pregnant. In a second experiment with 11 sows, the GnRH dosage was decreased to 1.5 ig every hour for 7 days, initiating treatment on the 31st day of lactation. All of the sows showed estrus (3.8 days after initiation of treatment) and 85% got pregnant, concluding that this LHRH treatment during lactation induced follicular development, estrus and ovulation (Cox and Britt, 1982 and De Rensis *et al.*, 1991).

Use of Exogenous Gonadotrophins: Exogenous hormone therapy as a means of inducing estrus during lactation has limited success and has often involved a series of injections which is both time consuming and impractical (Crighton, 1970ab and Guthrie *et al.*, 1978).

Administering gonadotrophins during lactation may induce ovulation more predictably than release factors do. However, the response varies with the stage of lactation at which the sow is treated (Kirkwood and Thacker, 1998). Ovulation has been induced in days 7 to 15 post partum, but subsequent pregnancy rates have been uniformly poor (Guthrie *et al.*, 1978 and Hausler *et al.*, 1980).

Cole and Hughes (1946) induced ovulation in 96% of sows that received pregnant mare serum gonadotrophin (PMSG) at 40 days post partum but few sows ovulated when injected prior to that day. Crighton (1970b) demonstrated that when PMSG was administered after 21 days post partum, the majority of the sows did not come into heat. But if the dosage of PMSG (1500 U.I.) was combined with the partial separation of the litter from the 21st day of lactation during 12 hours daily for three days, 83% of the treated sows showed estrus signs, saving 25 days in the period between farrowings when compared with those sows that were mated after weaning. The subsequent litter size was unaffected. In other words, Crighton (1970b) was unable to achieve a consistent response with either partial weaning or with the injection of PMSG, but when both treatments were combined better results were obtained. These experiments contrast with later work from Foxcroft *et al.* (1987). These authors evaluated the effects of a combination of split weaning and gonadotrophin treatment at weaning and reported that gonadotrophin treatment had no significant effect on any aspect of reproductive performance, but split weaning in mid lactation was associated with shorter weaning to estrus interval and increased litter size in the subsequent farrowing.

Britt *et al.* (1985) reviewed experiments concerning the application of gonadotrophins to lactating sows. It appears the later in lactation the gonadotrophins are used the better the response. Fourteen percent of sows responded to treatment between the 1st and the 5th day of lactation, whereas treatment between 30 and 36 days post partum produced a 64% and 72% response, respectively. Britt *et al.* (1997) tested three treatment regimens in 40 primiparous and 83 multiparous hybrid lactating sows nursing 8 to 12 piglets. They concluded that none of the control primiparous or multiparous sows ovulated during the 21 days of lactation period. Treatment with HCG alone on the day of farrowing induced ovulation in 90% of primiparous and 71% of multiparous sows. Treatment with PG600 on day 4 and HCG on day 7 was more successful in inducing ovulation in primiparous (90%) than multiparous (55%) sows. In contrast, treatment with PG600 on day 11 followed by HCG on day 14 stimulated more multiparous than primiparous sows to ovulate during lactation (95 Vs. 70%).

Yet, the results in the use of gonadotrophins are not consistent. Costa and Varley (1995) found no signs of lactational estrus when treating sows with PMSG and HCG after 17 days post partum and separating them from their litters for 3 to 12 hours daily and exposing them to the boar; there were any differences in the size of the subsequent litter. Moreover, Kirkwood and Thacker (1998) have advised against the protocol of gonadotrophin treatment at 28 days of lactation. Ovulation and subsequent pregnancy were successfully established and although pregnancy concurrent with lactation did not adversely affect the performance of the suckled litter or the size of the subsequent litter, there was a lower farrowing rate of induced sows and a potential for unpredictable returns to estrus.

Another way of inducing lactational ovulation has been by treating sows with an LH-like hormone (HCG) soon after parturition to induce ovulation and formation of the corpus luteum that can be lysed using PGF₂ analog causing the sows to start a new cycle and return to estrus. This strategy is experimental and since a number of sows do not

ovulate in response to the HCG and the CL formed on those that do may not lyse in response to PGF₂ treatment, it will remain experimental unless improvements in efficiency are made (Armstrong *et al.*, 1999 and Kirkwood *et al.*, 1999).

From these data we conclude that the response to the use of gonadotrophins varies according to the stage of lactation, the parity of the sow, if they are primiparous or multiparous, the dosage applied and the management of the animals.

Use of Estrogens: Cox *et al.* (1988) gave estradiol benzoate (EB) at the end of the second, third or fourth week of lactation. Only one sow out of four in the first group and 4 out of 5 sows in the other groups showed estrus; only one animal ovulated in the experiment (estradiol treatment at the end of the second week). On the other hand, Sesti and Britt (1993) with the use of estradiol benzoate shots induced lactational estrus in 95 and 100% of treated sows on the 14th or 28th day of lactation, respectively; however, ovulatory response was not successful, suggesting that suckling inhibited the ovarian response to a LH surge induced by EB by yet undetermined mechanisms.

Use of Opioid Peptides: During lactation the opioid peptides are closely linked to the inhibition of GnRH release and consequently to LH and FSH (Armstrong *et al.*, 1988a; Barb *et al.*, 1986 and Mattioli *et al.*, 1986). Acute administration of morphine at 25 days post partum prevented the increase of LH secretion associated with partial weaning. On the other hand, chronic administration of morphine delayed the onset of estrus after weaning, presumably through suppression of LH secretion (Armstrong *et al.*, 1988b). Contrary, the infusion of naloxone in lactating sows caused an increase of LH secretion and a decrease of peripheral prolactin (Armstrong *et al.*, 1988a; Barb *et al.*, 1986 and Mattioli *et al.*, 1986).

Conclusion

Reproductive management has become one of the major areas of interest in industrialized porcine production. We have observed how in theory, although conflicting evidence, the reproductive efficiency of the sow can be increased if the advantages of lactational estrus are utilized and the sow is successfully pregnant while she is still lactating. However, if this were to occur commercially the lactational estrus in the sow should be present in a high percentage of females while maintaining the normal parameters of survival and growth of the piglets, without compromising the subsequent reproductive cycle of the sows in terms of fertility and litter size and weight. We have to remember that the management of the lactating sow affects total herd productivity by influencing milk production and subsequent reproductive performance.

Worldwide porcine production has suffered drastic changes. During the last decade there has been a clear tendency to reduce the lactation length (Dial *et al.*, 1995 and Becerril *et al.*, 1996). In the beginning the lactations were reduced to eliminate or control diseases, afterwards this was dismissed when it was surmised that if the period of lactation become shorter, the number of litters and the number of piglets weaned/farrowing crate per sow per year were higher. Yet, sows that are allowed to lactations shorter than 21 days have a pressure for intense production, thus resulting in a shorter longevity (Koketsu *et al.*, 1996a and Xue *et al.*, 1996ab, 1997), putting at risk the immunity of the herd (Gadd, 1998). Cole *et al.* (1972) stated that sows subjected to ultra-early weaning presented a higher incidence of ovarian cysts and anovulatory follicles. Koketsu *et al.* (1996b) showed that early weaning elicits alterations in the sows and the piglets, while a decrease in fertility rate and subsequent litter size has been observed as well (Xue *et al.*, 1993; Koketsu *et al.*, 1994 and Belstra *et al.*, 1999). Besides, there has been an increase in the weaning to estrus interval (Xue *et al.*, 1993, 1996ab; Koketsu *et al.*, 1996b and Trujillo *et al.*, 1997), increasing the open days and reducing the number of farrowings/sow/year. In this sense it is worth to mention that this results depend on the lactation length. It appears that those sows with lactation lengths of more than 12-14 days have a significantly higher first service-farrowing rate when compared with those with a lactation length of less than 12-14 days. This does, however, indicate that sows can be weaned at ages as early as 12-14 days and not suffer a significant reduction in subsequent farrowing rate (Mabry *et al.*, 1996 and Britt, 1996).

Behavioral problems in the piglets that have been weaned precociously (*e.g.* Algers, 1984; Robert *et al.*, 1999 and Worobec *et al.*, 1999) are another concern of these systems. The behavioral implications of weaning at 3 weeks of age had been observed by Fraser (1978), who conclude that piglets have a difficulty lying together comfortably compared with piglets weaned at 6 weeks of age. Dybkjær (1992) observed redirected oral behavior in piglets weaned at 4 weeks, such as belly-nosing and oral manipulation of pen-mates' ears, tails and other body parts and suggested these were possibly indicators of stress. There is evidence that weaning at young ages can result in piglets developing behavior patterns and physiological changes that are suggestive of reduced welfare (Worobec *et al.*, 1999); the European Economic Community has banned weaning at <21 days suggesting it is detrimental to sow welfare. However, there is no evidence to indicate that early weaning is a greater stressor on sows than weaning after a conventional lactation length. In fact short lactations should minimize loss of body reserves (fat

and muscle), which should theoretically improve sow welfare and reproductive performance (Belstra, 1999). The increasing use of shorter lactations in animals subjected to intensive systems has obligated us to propose alternative systems of production. The induction of conception during lactation could in the future eliminate the use of shorter lactations to increase the productivity of the sow without risking longevity, health and physical condition. It also could be the key to shorten the periods between farrowings without subjecting the animals to pressures of production and respecting their welfare and at the same time, cutting down the costs of the facilities in which the lactating-pregnant pigs are housed.

We still have to study the different factors that contribute the induction of lactational estrus in the sow in a practical manner for the producer. As we conclude in this review, the task is not easy. The use of exogenous hormones has not proven to be quite successful. Although there are natural methods for lactational estrus induction, these never act separately; there is a potential managing sows in groups exposed to boars, but at the same time we do not know if this estrus is due exclusively to both factors or if it has to do with an environmental or nutritional interaction, since the animals are subjected to more natural systems of housing, with an enhanced and richer environment. Three features appeared crucial to the induction of estrus during lactation: First, the sows are allowed to lactate for longer (>45 days) than is allowed in most current commercial farms in the world. Secondly, the sows are group housed during lactation with a mature boar present. Thirdly, they are provided with generous feeding which minimizes weight loss. Therefore, few farmers would use this technique for improving pig welfare and productivity at the same time. These would be both the outdoor farms, the family pig farms or those who have lactation length constraints.

Acknowledgements

Daniel Mota greatly acknowledges the financial support of CONACyT (Consejo Mexicano de Ciencia y Tecnología, Mexico. Project number 4214P-B9607.) while writing this article.

References

- Algers, B., 1984. Early weaning and cage rearing of piglets: influence on behaviour. *Zbl. Vet. Med., Reihe A.* 31:14-24.
- Algers, B., 1991. Group housing of farrowing sows. Health aspects on a new system. 7th International Congress on Animal Hygiene. Leipzig, pp. 851-857.
- Algers, B., A. Madej, S. Rojanasthien and K. Uvnäs-Moberg, 1991. Quantitative relationships between suckling-induced teat stimulation and the release of prolactin, gastrin, somatostatin, insulin, glucagon and vasoactive intestinal polypeptide in sows. *Vet. Res. Comm.*, 15:395-407.
- Alonso-Spilsbury, M. and L. Mayagoitia, 1998. Conducta materna de la cerda pelón mexicano en condiciones agro-silvo-pastoriles. *Memorias del XXXIII Congreso Nacional AMVEC*. Guanajuato, México, pp:1-3.
- Alonso-Spilsbury, M., N.R. Ramírez and R.D. Mota, 1998. Estro lactacional de la cerda pelón mexicano mantenida en condiciones agro-silvo-pastoriles. *Memorias del XXXIII Congreso Nacional AMVEC*. Guanajuato, México, pp: 136-137.
- Anon, 1984. Apareando durante la lactancia. *Industria Porcina* (Ene.).
- Armstrong, J.D., R.R. Kraeling and J.H. Britt, 1988a. Effects of naloxone or transiently weaning on secretion of LH and prolactin in the lactating sow. *J. Reprod. Fert.*, 83:301-308.
- Armstrong, J.D., R.R. Kraeling and J.H. Britt, 1988b. Morphine suppresses luteinizing hormone concentrations in transiently weaned sows and delayed onset of estrus after weaning. *J. Anim. Sci.*, 66: 2216-2223.
- Armstrong, T.A., W.L. Flowers and J.H. Britt, 1999. Control of weaning-to-estrus interval in sows using gonadotropins and prostaglandins during lactation. *J. Anim. Sci.*, 77:533-2539. (Cited by Belstra, 1999).
- Baker, N.L., H.L. Woehling, L.E. Casida and R.H. Grummer, 1953. Occurrence of oestrus in sows following parturition. *J. Anim. Sci.*, 12:33-38.
- Barb, C.R., R.R. Kraeling, G.B. Rampacek and C.S. Whisnant, 1986. Opioid inhibition of LH secretion in the post-partum lactating sow. *Biol. Reprod.*, 35:368-371.
- Becerril, J., G.R. Ortega and N.J. Conejo, 1996. Efecto de lactancias cortas e intervalo destete servicio sobre la productividad de las cerdas. *Memorias XXXI Congreso Nacional AMVEC*, Veracruz México, p. 112.
- Belstra, B.A., B.T. Richert, M.A. Diekman, J.W. Frank, D.C. Kendall and W.L. Singleton, 1999. Effect of lactation length and exogenous progesterone/estradiol-17 β on embryo survival in multiparous sows. *J. Anim. Sci.*, 77 (Suppl. 2): 48.
- Belstra, B., 1999. Management strategies to counteract the negative effect of short lactation lengths (early weaning) on subsequent sow reproductive performance. *Proc. North Carolina Healthy Hogs Seminar*. pp:10.
- Booman, P. and D.F.M. Vander Wiel, 1980. Lactational anoestrus in the pig: possible relationship with hyperprolactinaemia. Report B-157. Instituut voor veeteeltkundig onderzoek 'Schoonoord' Zeist. The Netherlands. 96 pp. (Cited by Kemp, 1998).
- Britt, J.H., 1996. Biology and management of the early weaned sow. *Proceedings of the Am. Ass. Swine Practitioners 27th Annual Meeting*. March 2-5, Nashville, TN, pp. 417-426.

- Britt, J.H., J.D. Armstrong, N.M. Cox and K. Esbenshade, 1985. Control of follicular development during and after lactation in the sow. *J. Reprod. and Fert. Suppl.* 33:37-54.
- Britt, J.H., W.L. Flowers and T.A. Armstrong, 1997. Induction of ovulation in early weaned sows. *Proceedings of the Am. Ass. Swine Practitioners 28th Annual Meeting*. pp:33-35.
- Bryant, M.J., P. Rowlinson, A.M. Van Der Steen, 1983a. A comparison of the nursing and suckling behaviour of group- and individually- housed sows and their litters. *Anim. Prod.*, 36: 445-451.
- Bryant, M.J., G. Palmer, D.J. Petherick, P. Rowlinson, 1983b. Lactational oestrus in the sow. 4. Variation in the incidence and timing of lactational oestrus in groups of sows. *Anim. Prod.*, 36: 453-460.
- BØE, K., 1994. Variation in maternal behavioural and production of sows in integrated loose housing systems in Norway. *Appl. Anim. Behav. Sci.*, 41:53-62.
- Burger, J.F., 1952. Sex physiology of pigs. *Onderstepoort. J.Vet. Res. Suppl.*, 2:3-218.
- Castrén, H., B. Algers and P. Jensen, 1989. Occurrence of unsuccessful sucklings in newborn piglets in a semi-natural environment. *Appl. Anim. Behav. Sci.*, 23: 61-73.
- Castrén, H., B. Algers, A.M. De Pasillé, J. Rushen and K. Uvnäs-Moberg, 1993. Pre-parturient variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest building in sows. *Appl. Anim. Behav. Sci.*, 38: 91-102.
- Cole, D.J.A., P.H. Brooks and R.M. Kay, 1972. Lactational oestrus in the sow. *Vet. Rec.*, 90: 681-683.
- Cole, H.H. and E.H. Hughes, 1946. Induction of estrus in lactating sows with equine gonadotropin. *J. Anim. Sci.*, 5:25-29.
- Cosgrove, J.R. J.E. Tilton, M.G. Hunter and G.R. Foxcroft, 1992. Gonadotrophin-independent mechanisms participate in ovarian responses to realimentation in feed-restricted prepuberal gilts. *Biol. Reprod.*, 47:736-745.
- Cosgrove, J.R. and G.R. Foxcroft, 1996. Nutrition and reproduction in the pig: ovarian aetiology. *Anim. Reprod. Sci.*, 42:131-141.
- Costa, A.N. and M.A. Varley, 1995. The effects of altered suckling intensity, boar exposure in lactation and gonadotropins on endocrine changes, fertility and the incidence of lactational oestrus in multiparous sows. *Anim. Sci.*, 60:485-492.
- Cox, N.M. and J.H. Britt, 1982. Pulsatile administration of gonadotropin releasing hormone to lacting sows: Endocrine changes associated with induction of fertile estrus. *Biol. Reprod.*, 27:1126-1137.
- Cox, N.M., J.H. Britt, W.D. Armstrong and H.D. Alhusen, 1983. Effect of feeding fat and altering weaning schedule on rebreeding in primiparous sows. *J. Anim. Sci.*, 56:21-29.
- Cox, N.M., M.J. Stuart, T.G. Althen, W.A. Bennett and H.W. Miller, 1987. Enhancement of ovulation rate in gilts by increasing dietary energy and administering insulin during follicular growth. *J. Anim. Sci.*, 64: 507-516.
- Cox, N.M., J.L. Ramírez, I.A. Matamoros and W.A. Bennett, 1988. Estrogen induces estrus unaccompanied by a preovulatory surge in luteinizing hormone in suckled sows. *Biol. Reprod.* 38: 592-596.
- Crighton, D.B., 1970a. Induction of pregnancy during lactation in the sow. *J. Reprod. Fert.*, 22:223-231.
- Crighton, D.B., 1970b. The induction of pregnancy during lactation in the sow: the effects of a treatment imposed at 21 days of lactation. *Anim. Prod.*, 12:611-617.
- De Rensis, F., M.G. Hunter, S.A. Grant, R.T. Lancaster and G.R. Foxcroft, 1991. Expression of messenger RNAs encoding insulin-like growth factor I-II insulin like growth factor binding protein-2 in bovine endometrium during the estrous cycle and early pregnancy. *Biol. Reprod.*, 126: 975-982.
- De Rensis, F., J.R. Cosgrove and G.R. Foxcroft, 1993. Luteinizing hormone and prolactin responses to naloxone vary with stage of lactation in the sow. *Biol. Reprod.*, 48:970-976.
- De Rensis, F., H.J. Willis, J.R. Cosgrove, S. Hofalker and G.R. Foxcroft, 1996. Interaction between suckling and morphine administration in the regulation of LH and prolactin secretion in the sow. *Proc. 14th International Pig Vet. Soc. Congress. Bologna, Italy*, pp:613.
- Dial, G., Y. Koketsu, J.L. Xue, T. Lucia and P. Bahnson, 1995. Optimizing breeding performance in early weaning systems: factors affecting the reproductive response to lactation length. *Recent Advances in Swine Prod. and Health*, 5:101-112.
- Dritz, S.S., J.L. Nelssen, R.D. Goodband, M.D. Tokach and M.M. Chengappa. 1994. Application of segregated early weaning technology in the commercial swine industry. *Compend. Cont. Educ. Pract. Vet.*, 16: 677.
- Duggan, R.T., M.J. Bryant and F.J. Cunningham, 1982. Gonadotrophin, total oestrogen and progesterone concentrations in the plasma of lactating sows with particular reference to lactational oestrus. *J. Reprod. Fert.*, 64:303-313.
- Dusza, L. and J.E. Tilton, 1990. Role of prolactin in the regulation of ovarian function in pigs. *J. Reprod. Fert. Suppl.*, 40:33-45.
- Dybckjær, L., 1992. The identification of behavioural indicators of stress in early weaned piglets. *Appl. Anim. Behav. Sci.*, 35:135-147.
- Edwards, S. and G.R. Foxcroft, 1983. Endocrine changes in sows weaned at two stages of lactation. *J. Reprod. Fert.*, 67:161-172.

- Einarsson, S. and T. Rojittikhun, 1993. Effect of nutrition on pregnant and lactating sows. *J. Reprod. Fert. Suppl.*, 48:229-239.
- Foxcroft, G.R., H.J. Shaw, M.G. Hunter, P.J. Booth and R.T. Lancaster, 1987. Relationship between luteinizing hormone, follicle-stimulating hormone, prolactin secretion and ovarian follicular development in weaned sows. *Biol. Reprod.*, 36:175-191.
- Foxcroft, G.R., N. Brooks, J. Challis, A. Mcneilly and C. Doberska, 1992. Nutritional and lactational regulation of fertility in sows. *J. Reprod. and Fertility*. 45 (Suppl.): 113-125.
- Fraser, D., 1978. Observation on the behavioural development of suckling and early-weaned piglets during the first six weeks after birth. *Anim. Behav.*, 26:22-30.
- Gadd, J., 1998. Inmunidad natural: nuestro talón de Aquiles. *Porcicultores*. 1:10-15.
- Graves, W.E., J.W. Lauderdale, R.L. Kirkpatrick, N.L. First and L.E. Casida, 1967. Tissue changes in the involuting uterus of the postpartum sow. *J. Anim. Sci.*, 26:365-369.
- Guthrie, H.D., V.G. Pursel and L.T. Frobish, 1978. Attempts to induce conception in lactating sows. *J. Anim. Sci.*, 47:1145-1151.
- Hausler, C.L., H.H. Hodson, D.C. Kuo, T.J. Kinney, V.A. Rauwolf and L.E. Strack, 1980. Induced ovulation and conception in lactating sows. *J. Anim. Sci.*, 50:773-778.
- Hays, V.W., J.L. Krug, G.L. Cromwell, R.H. Dutt and D.D. Kratzer, 1978. Effect of lactation length and dietary antibiotics on reproductive performance of sows. *J. Anim. Sci.*, 46:884-891.
- Henderson, R. and P.E. Hughes, 1984. The effects of partial weaning, movement and boar contact on the subsequent reproductive performance of lactating sows. *Anim. Prod.*, 39:131-135.
- Henderson, R. and A. Stolba, 1989. Incidence of oestrus and oestrus trends in lactating sows housed in different social and physical environments. *Appl. Anim. Behav. Sci.*, 22:235-244.
- Holmes, M.A., C. Maughan, A. Paterson, G. Bryant-Greenwood, G. Rice and P.E. Hartmann, 1988. The uptake of glucose by the mammary glands of lactating sows. *Proc. of the Nutrition Society of Australia* 13, 113. (Cited by Hartmann and Holmes, 1989).
- Holt, H.A., J.S. Richards, A.R. Midgley and L.E. Reichert, 1976. Effect of prolactin on LH receptor in rat luteal cells. *Endocrinology*, 98:1005-1013.
- Hughes, P.E. and M.A. Varley, 1980. Reproduction in the Pig. Butterworths, U. K. pp. 141-144.
- Hultén, F., A.M. Dalin, N. Lundheim and S. Einarsson, 1995a. Ovulation frequency among sows group-housed during late lactation. *Anim. Reprod. Sci.*, 39:223-233.
- Hultén, F., A.M. Dalin, N. Lundheim and S. Einarsson, 1995b. A field study on group housing of lactating sows with special reference to sow health at weaning. *Acta Vet Scand*, 36:201-212.
- Jensen, P., 1986. Observations on the maternal behaviour of free-ranging domestic pigs. *Appl. Anim. Behav. Sci.*, 16:131-142.
- Jensen, P. and G. Stangel, 1992. Behaviour of piglets during weaning in a semi-natural enclosure. *Appl. Anim. Behav. Sci.*, 33:227-238.
- Kemp, B., 1998. Lactational effects on the endocrinology of reproduction. In: Verstegen, M.W.A., Moughan, P.J. and Schrama, J.W. (Eds). *The Lactating Sow*. Wageningen Pers. The Netherlands. pp: 241-257.
- Kendall, J.Z., G.E. Richards and L.N. Shih, 1983. Effect of haloperidol, suckling, oxytocin and hand milking on plasma relaxin and prolactin concentration in cyclic and lactating pigs. *J. Reprod. Fert.*, 69:271-277.
- King, V.L., Y. Koketsu, D. Reeves, J.L. Xue and G.D. Dial, 1998. Management factors associated with swine breeding-herd productivity in the United States. *Prev. Vet. Med.*, 35:255-264.
- Kirkwood, R.N. and P.A. Thacker, 1998. Induced estrus and breeding during lactation: Effects on sow and litter performance. *Swine Health and Production*. 6:95-98.
- Kirkwood, R.N., S.C. Henry, L.M. Tokach and G.R. Foxcroft, 1999. Human chorionic gonadotropin at parturition fails to consistently induce ovulation in sows. *SHAP*. 7: 69-71. (Cited by Belstra, 1999).
- Koketsu, Y., G.D. Dial, W.E. Marsh, J.E. Pettigrew and V.L. King, 1994. Feed intake during lactation and subsequent reproductive performance of sows. *J. Anim. Sci.* 72 (Suppl. 1): 1283.
- Koketsu, Y., G.D. Dial and T. Lucia, 1996a. A profile of commercial farms in the USA early weaning systems. 14th International Pig Veterinary Society Congress Proc. Bologna, Italy, pp: 475.
- Koketsu, Y., G.D. Dial and V.L. King, 1996b. Influence of various factors on the relationship between lactation length and subsequent litter size on farms using early weaning. 14th International Pig Veterinary Society Congress Proc. Bologna, Italy, pp: 484.
- Kunavongkrit, A.S., S. Rojanasthien and R.B. Ogle, 1985. Effect of fractionated weaning on hormonal patterns and weaning to oestrus interval in sow. *Swedish J. Agric. Res.*, 15:39-44.
- Loseth, K.J. and B.G. Crabo, 1994. Restricted suckling for rebreeding of lactating sows. *Proc. Intl. Soc. of Animal Hygiene (ISAH)*. Mpls, Minn. pp. AW33-AW36.
- Mabry, J.W., M. S. Culbertson and D. Reeves, 1996. Effects of lactation length on weaning-to-first-service interval, first-service farrowing rate and subsequent litter size. *Swine Health and Prod.* 4:185-187.

- Malven, P.V., 1986. Inhibition of pituitary LH release resulting from endogenous opioid peptides. *Dom. Anim. Endocr.*, 3:135-144.
- Marshall, F.H.A. and J. Hammond, 1937. Fertility and animal breeding. *Bull. Minist. Agric. Fish Fd. Land* 32. (Cited by Crighton, 1970).
- Marsteller, T.A., G.A. Armbruster, D.B. Anderson, A.J. Wuethrich, J.L. Taylor and J.T. Symanowski, 1997. Effect of lactation length on ovulation rate and embryo survival in swine. *Swine Health and Prod.*, 5:49-56.
- Matte, J.J., C. Pomar and W.H. Close, 1992. The effect of interrupted suckling and split-weaning on reproductive performance of sows: a review. *Livest. Prod. Sci.*, 30:195-212.
- Mattioli, M., F. Conte, G. Galeati and E. Seren, 1986. Effect of naloxone on plasma concentration of prolactin and luteinizing hormone in the lactating sow. *J. Reprod. Fert.*, 76:167-173.
- Meurer, K.A., N.M. Cox, I.A. Matamoros and R.C. Tubbs, 1991. Decreased follicular steroids and insuline-like growth factor-I and increased atresia in diabetic gilts during follicular growth stimulated with PMSG. *J. Reprod. Fert.*, 91:187-196.
- Moser, H., 1989. Reproductive Performance of Domestic Pigs Kept in Family Groups. Ph D Dissertation. Universität Zürich. (Cited by Stolba *et al.*, 1990).
- Mota, D., M. Alonso-Spilsbury, L. Mayagoitia, M.E. Trujillo, J. Valencia and R. Ramírez-Necoechea, 2002. Lactational estrus induction in the Mexican hairless sow. *Anim. Repr. Sci.*, 72: 115-124.
- Murphy, B.D. and K. Rajkumar, 1985. Prolactin as a luteotrophin. *Can. J. Pharmacol.*, 63:257-264.
- Newton, E.A., J.S. Stevenson, J.E. Minton and L.D. Davies, 1987a. Endocrine changes before and after weaning in response to boar exposure and altered suckling in sows. *J. Reprod. Fert.*, 81:599-609.
- Newton, E.A., J.S. Stevenson and L.D. Davies, 1987b. Influence of duration of litter separation and boar exposure on estrous expression of sows during and after lactation. *J. Anim. Sci.*, 65:1500-1506.
- Petchey, A.M. and G.M. Jolly, 1979. Sow service in lactation: an analysis of data from one herd. *Anim. Prod.*, 29:183-191.
- Petchey, A.M. and P.R. English, 1980. A note on the effects of the boar presence on the performance of sows and their litters when penned in groups in late lactation. *Anim. Prod.*, 32:107-109.
- Petchey, A.M., T.L. Dodsworth and P.R. English, 1978. The performance of sows and litters penned individually or grouped in late lactation. *Anim. Prod.*, 27:15-221.
- Pettigrew, J.E. and M.D. Tokach, 1993. Metabolic influences on sow reproduction. *Pig News and Information*. 14: 69N-72N.
- Poretsky, L. and M.F. Kalin, 1987. The gonadotropic function of insulin. *Endocrine Reviews*. 8: 132-141.
- Quesnel, H. and A. Prunier, 1995. Endocrine bases of lactational anoestrus in the sow. *Reprod. Nutr. Develop.*, 35:395-414.
- Riley, J.E., S.A. Edwards, P.H. Simmins, C.M. Shepherd and M.A. Brade, 1985. The effects of fractionated weaning on sow productivity. *Proc. 2nd Intl. Conf. Pig Repr. Columbia, USA*, pp: 71.
- Robert, S., D. Weary and H. Gonyou, 1999. Segregated early weaning and welfare of piglets. *J. Appl. Anim. Welf. Sci.*, 2:31-40.
- Rojkittikhun, T., S. Einarsson, L.E. Edqvist, K. Uvnäs-Moberg, N. Lundeheim, 1992. Relationship between lactation-associated body weight loss, levels of metabolic and reproductive hormones and weaning-to-oestrus interval in primiparous sows. *J. Vet. Med.*, 39:426-432.
- Rowlinson, P. and M.J. Bryant, 1981. Lactational oestrus in the sow. 1. The effect of interval between farrowing and grouping on the incidence and timing of lactational oestrus in sows. *Anim. Prod.*, 32:315-323.
- Rowlinson, P. and M.J. Bryant, 1982a. Lactational oestrus in the sow. 3. The influence of feeding level upon the occurrence of fertile oestrus in lactating sows. *Anim. Prod.*, 3:49-53.
- Rowlinson, P. and M.J. Bryant, 1982b. Lactational oestrus in the sow. 2. The influence of group-housing, boar presence and feeding level upon the occurrence of oestrus in lactating sows. *Anim. Prod.*, 34:283-290.
- Rowlinson, P., M.J. Bryant and H.G. Boughton, 1974. Sows mated during lactation: observations from a commercial unit. *Proc. Br. Soc. Anim. Prod.*, 3:93 (Abstract).
- Rowlinson, P., H.G. Boughton and M.J. Bryant, 1975. Mating of sows during lactation: observations from a commercial unit. *Anim. Prod.*, 21:233-241.
- Rushen, J., G. Foxcroft and A.M. De Passillé, 1993. Nursing-induced changes in pain sensitivity, prolactin and somatotropin in the pig. *Physiol and Behav*, 53:265-270.
- Self, H.L. and R.H. Grummer, 1958. The rate and economy of pig gains and the reproductive behaviour in sows when litters are weaned at 10 days, 21 days or 56 days of age. *J. Anim. Sci.*, 17:862-868.
- Sesti, L.A.C. and J.H. Britt, 1993. Influence of stage of lactation, exogenous luteinizing hormone-releasing hormone and suckling on estrus, positive feedback of luteinizing hormone and ovulation in sows treated with estrogen. *J. Anim. Sci.*, 71:989-998.
- Shaw, H.J., 1984. Control of Ovarian Function in Lactating and Weaned Sows. Ph D. Thesis. Nottingham, U. K. University of Nottingham.

- Smith, D.M., 1961. The effect of daily separation of sows from their litters upon milk yield, creep intake and energetic efficiency. *N. Z. J. Agric. Res.*, 4:232-245.
- Stevenson, J.S. and J.H. Britt, 1980. Luteinizing hormone, total oestrogens and progesterone secretion during lactation and after weaning in sows. *Theriogenology*, 1:453-462.
- Stevenson, J.S. and D.L. Davis, 1984. Influence of reduced litter size and daily litter separation on fertility of sows at 2 to 5 weeks postpartum. *J. Anim. Sci.*, 59:284-293.
- Stevenson, J.S., G.R. Cox and J.H. Britt, 1981. Role of the ovary in controlling luteinizing hormone, follicle stimulating hormone and prolactin secretion during and after lactation in pigs. *Biol. Reprod.* 24:341-353.
- Stolba, A., 1981. A family system in enriched pens as a novel method of pig housing. In: R. Ewbank (Ed.). *Alternatives to Intensive Husbandry Systems*. UFAW Conf. Potters, Bar. pp:52-67.
- Stolba, A., 1982. Designing pig housing conditions according to patterns of social structure. *Scottish Agricultural Colleges and Meat Livestock Commission Pig Conference*, Perth.
- Stolba, A., 1984. Lactational oestrus in sows kept in rich environments. *Proc. Intl. Congr. on Applied Ethology in Farm Animals*. J. Unshelm, G. van Putten y K. Zeeb (eds.). Kiev, Germany, pp:226-228.
- Stolba, A., R. Henderson and B. Wechsler, 1990. The influence of different social and physical environments on the incidence of lactational oestrus in sows. *Appl. Anim. Behav. Sci.*, 27:269-276.
- Svajgr, A.J., V.W. Hays, G.L. Cromwell and R.H. Dutt, 1974. Effect of lactation duration on reproductive performance of sows. *J. Anim. Sci.*, 38:100-105.
- Tokach, M., J. Pettigrew, G. Dial, B. Wheaton and Y. Koketsu, 1992. Characterization of luteinizing hormone secretion in primiparous lactating sow: relationship to blood metabolites and return-to-estrus interval. *J. Anim. Sci.*, 70:2195-2201.
- Trujillo, O.M.E., Q.L.A. Zarco, D.J.M. Doporto and F.A. Becerra, 1997. Efecto de la disminución de los días de lactancia sobre la eficiencia reproductiva. *Memorias del XXXII Congreso Nacional AMVEC*. Ixtapa Zihuatanejo, pp:148.
- Varley, M.A. and T. Atkinson, 1985. Weaning at birth: the effect on reproduction of the sow. *Anim. Prod.*, 41:375-382.
- Varley, M.A. and G.R. Foxcroft, 1990. Endocrinology of the lactating and weaned sow. *J. Reprod. Fert. Suppl.*, 40:47-61.
- Vesseur, P.C., 1997. Causes and Consequences of Variation in Weaning to Oestrus Interval in the Sow. Ph D Thesis. Agricultural Univ. Wageningen. The Netherlands, pp:165.
- Vesseur, P.C., J.C. Plagge and R.H.J. Scholten, 1995. Induction of oestrus in 'scharrel' sows during lactation using natural stimuli. *Proefstation voor de Varkenshouderij*. 1-136:28.
- Warnick, A.C., L.E. Casida and R.H. Grummer, 1950. The occurrence of estrus and ovulation in post partum sows. *J. Anim. Sci.*, 9:60-72.
- Wechsler, B., 1995. The incidence of lactational oestrus in a field trial with sows kept in family groups. *KTBL Schrift*, 370:247-256.
- Wechsler, B., 1996. Rearing pigs in species-specific family groups. *Animal Welfare*, 5:25-35.
- Worobec, E.K., I.J.H. Duncan and T.M. Widowski, 1999. The effects of weaning at 7, 14 and 28 days on piglet behaviour. *Appl. Anim. Behav. Sci.*, 62:173-182.
- Xue, J.L., G.D. Dial, W.E. Marsh, P.R. Davis and H.W. Mommont, 1993. Influence of lactation length on sow productivity. *Livest. Prod. Sci.*, 34:253-265.
- Xue, J.L., G.D. Dial, W.E. Marsh and T. Lucia, 1996a. Early weaning: a risk factor for sow longevity. 14th International Pig Veterinary Society (IPVS) Congr. Proc. Bologna, Italy, pp: 478.
- Xue, J.L., P. Bahnson and G.D. Dial, 1996b. Factors influencing the reproductive performance of early weaned sows. 14th IPVS Congr. Proc. Bologna, Italy, pp:471.
- Xue, J.L., G.D. Dial, W.E. Marsh and T. Lucia, 1997. Association between lactation length and sow reproductive performance and longevity. *JAVMA*. 210:935-938.