

/INFLUENCE OF ALTERED SUCKLING AND BOAR EXPOSURE ON SOWS/
ESTROUS RESPONSE AND ENDOCRINE CHANGES ASSOCIATED WITH/
LACTATIONAL AND POSTWEANING ESTRUS

by

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LITERATURE REVIEW

Estrous Expression in Sows After Parturition and Weaning

Sexual behavior following parturition has been described in sows. After the first week of lactation incidence of spontaneous estrus is 4 to 7% (Burger, 1952; Loebel and Schlegel, 1972). Estrus that occurs within 1 wk postpartum (pp) is generally found to be infertile as sows fail to ovulate (Warnick et al., 1950; Baker et al., 1953). Holness and Hunter (1975) observed pp estrus in one sow that was ovariectomized before parturition. They suggested that pp estrus was not related to ovarian estrogens, but possibly due to residual effects of the increased feto-placental estrogens before parturition.

Sows whose litters were weaned at birth had longer intervals from weaning to conception and farrowed fewer piglets than sows weaned after 34 to 42 d of lactation (Plonka et al., 1980; Varley and Atkinson, 1985). Other studies that examined altered lengths of lactation resulted in decreased intervals from weaning to estrus or decreased intervals from weaning to conception for longer lactations (Self and Grummer, 1958; Moody and Speer, 1971; Martinat-Botte et al., 1977; Allrich et al., 1979). Cole et al. (1975) found a curvilinear relationship between lactation length and the interval from farrowing to remating where reduction in 1 d of lactation resulted in .9 less days from farrowing to rebreeding.

Ovulation and fertilization rates were similar for sows bred after variable lactation lengths (Self and Grummer, 1958; Moody and Speer, 1971; Hays et al., 1978). However, embryonic mortality that resulted in decreased litter size at

the subsequent farrowing was greater in sows bred after shorter lactations (Cole et al., 1975; Hays et al., 1978; Allrich et al., 1979).

Mating of Sows During Lactation - Observations

Several management schemes incorporated into commercial sow herds promote the incidence of estrus during lactation (lactational estrus). Grouping sows with their litters, ad libitum feeding, and exposure of family groups to intact boars promote estrus and subsequent breeding of lactating females in some cases (Rowlinson and Bryant, 1976). Estimates of sows that respond (in terms of lactational estrus) to such management systems range from 50 to 100%, with conception rates varying from 78 to 85% (Eames, 1964; Rowlinson et al., 1975; Petchey and Jolly, 1979). Advantages of such practices include decreasing the farrowing interval, increasing sow productivity, and eliminating early weaning that alleviates the need for special care of very young pigs.

Induction of Pregnancy During Lactation

Two methods have been used to induce a fertile estrus during lactation in sows: social stimulation or hormonal therapy. Both systems result in reducing the inhibitory effects of lactation on ovarian activity and the provision of a direct stimulus for ovulation (Henderson and Hughes, 1984). Techniques are used to overcome the effects of the suckling stimulus on the hypothalamo-hypophyseal system to inhibit release of gonadotropins that normally induce follicular maturation and ovulation (Crighton and Lamming, 1969; Peters et al., 1969). Rowlinson and Bryant (1976) exposed groups of 3 to 8

sows and their litters to boars continuously from d 24 pp to weaning on d 42. In one experiment, 100% of the sows exhibited lactational estrus and when bred, 85% conceived. In this case, social stimulation in the form of "enriched family pens" induced sows to experience lactational estrus and pregnancy.

Hormonal treatments have consisted of combinations of gonadotropins injected at various pp intervals to induce ovarian follicular growth and ovulation. Pregnant mare serum gonadotropin (PMSG) at doses of 1,000 to 2,000 IU followed 72 to 96 h later by 500 to 1,000 IU human chorionic gonadotropin (hCG) generally induced lactational estrus (Crighton, 1970; Guthrie et al., 1978; Hausler et al., 1980; Martinat-Botte, 1975). Results were variable, however, especially when treatment was initiated early (less than day 15 pp) in lactation (Heitmann and Cole, 1956; Crighton, 1968; Hodson et al., 1981). When treatment with PMSG on d 23 was preceded by three 12-h intervals of sow-litter separation, incidence of estrus in lactating sows was 79.2% (Crighton, 1970). Induction of estrus also may depend on the size of the nursing litter at the time of treatment. Martinat-Botte (1975) found that the larger the litter suckled (5 vs 10 piglets), the lower the percentage of sows that respond to treatment (77.3 vs 46.8%). Hausler et al. (1980) found no effect of size of litter on sow response. This difference could be due to the fact that Hausler et al. (1980) used both PMSG and hCG in their treatment scheme, whereas Martinat-Botte (1975) used only PMSG. Perhaps the greater suckling intensity increased the inhibition of ovulation that is overcome subsequently by hCG.

Guthrie et al. (1978) induced ovulation in sows during the interval from d 14 to 17 pp using PMSG+hCG (400:200 IU) followed 72 h later by 500 mg of a

gonadotropin-releasing hormone (GnRH) analog. Pregnancy rates using this regimen were comparable with those using PMSG and hCG alone. Cox and Britt (1982a) induced pregnancy in sows during lactation using pulsatile administrations of GnRH. Sows exhibited estrus 3.9 d after GnRH treatment began with eight of twelve (67%) sows conceiving. Pulsatile administration of GnRH also was used to induce estrus and ovulation in seasonally anestrous primiparous sows (Armstrong and Britt, 1985). Presumably, GnRH treatment resulted in an increase in ovarian activity by increasing the frequency of gonadotropin release by the anterior pituitary because anestrous sows exhibited estrus 84 ± 5 h after hourly injections of GnRH were initiated. Armstrong and Britt (1985) and Cox et al. (1983b) suggested that postweaning anestrus may be due to an aberration in the brain, within or above the hypothalamus, because the hypothalamus and anterior pituitary of long-term anestrous sows responded to administration of estradiol and GnRH.

Factors of Management Affecting Lactational Estrus

Group vs Individual Housing

Grouping sows and their litters in multi-accommodation pens (Bryant et al., 1983a) appeared to induce estrus during lactation only when other factors were present as well. Sows grouped with their litters, but not exposed to boars, exhibit estrus much less frequently (3.0 vs 78.3%) than sows grouped together, exposed to boars, and fed ad libitum (Petchey et al., 1978; Rowlinson and Bryant, 1976; Rowlinson and Bryant, 1981; Bryant and Rowlinson, 1984).

Grouping sows and their litters changed the suckling behavior of the

piglets with differences most evident during the first 6 h after grouping (Petchey et al., 1978; Bryant and Rowlinson, 1984). Increased number of false nursing events, higher incidence of cross-suckling, and increased synchronization of true nursing events occurred more often in grouped than individually housed sows (Bryant and Rowlinson, 1984; Bryant et al., 1983a,b). However, there was no evidence that disrupting suckling behavior following grouping was responsible for inducing estrus because frequency and duration of suckling were similar between groups (Rowlinson et al., 1977).

Influence of the interval between farrowing and grouping on the incidence and timing of lactational estrus was variable. Rowlinson and Bryant (1981) found that sows grouped together at 25 d pp had shorter intervals to estrus than sows grouped at 10, 15, or 20 d pp (7.3 vs 10.8 d). They also noted that more synchrony of lactational estrus was seen within rather than between groups suggesting that sows may respond to female to female social interactions by synchronizing estrous cycles, as has been shown for menstrual cycles in women (McClintock, 1971). Whether or not this response is due in part to the influence of an olfactory controlling mechanism is not known (Russel et al., 1980).

Effect of Boar Exposure on Gilts and Sows

Attainment of Puberty in Gilts. Brooks and Cole (1970), Jensen et al. (1970), Zimmerman et al. (1974) and Mavrogenis and Robison (1976) have demonstrated that exposure of gilts to boars induced puberty earlier when gilts were moved out of confinement and compared to gilts not exposed to boars. Once daily or

continuous boar exposure produced comparable pubertal responses (Kopf et al., 1984; Caton et al., 1986b). Gilts subjected to boar exposure in confinement reached puberty at younger ages (190 vs 208 d), had shorter intervals to first ovulation (25.8 vs 44.0 d), and were in estrus more frequently (32.7 vs 4.9%) than those not exposed to boars (Thompson and Savage, 1978; Kopf et al., 1984). Kirkwood and Hughes (1980) found no difference in age at puberty or ovulation rate for gilts exposed to boars than those of controls (no boar exposure). However, boars used in the experiment were immature. Kirkwood and Hughes (1981) found subsequently that age of boar influenced advancement of puberty in gilts, with mature boars providing more stimulation than immature boars.

Ovulation rate does not appear to be influenced by the age at first estrus (Thompson and Savage, 1978; Kirkwood and Hughes, 1980). However, seasonal and genetic effects on age at puberty have been demonstrated (Thompson and Savage, 1978; Caton et al. 1986a). Mavrogenis and Robison (1976) found a significant interaction between season of birth and exposure to boars on the age of gilts at puberty. Brooks and Cole (1970) reported that puberty may actually be delayed if exposure to boars is initiated when gilts are too young.

Lactational Estrus in Sows. Boar exposure affected both pre-and postweaning estrous cyclicity in sows. Rowlinson and Bryant (1982a) reported that boar exposure, grouping of sows and their litters, and ad libitum feeding, stimulated sows to exhibit lactational estrus more frequently than any other treatment combination (78.3 vs 14.8%). Type and timing of boar exposure also may be critical to sow response. Petchey and English (1980) found that sows grouped

with their litters at 21 d pp and not exposed to a boar until 4 d post-grouping exhibited estrus less frequently (9.5 vs 84.2%) than that found in other studies (Bryant et al., 1983a,b; Bryant and Rowlinson, 1984). Similarly, Henderson and Hughes (1984) reported only 3.1% of sows partially weaned and either exposed to a boar (1 h/d) or an empty boar pen came into heat during lactation, whereas Walton (1986) found 3.0% of sows exposed to boars twice daily (30 min each) returned to estrus during lactation.

Prewaning exposure of sows to boars also may decrease the interval from weaning to estrus especially for multiparous sows. Petchey and English (1980) and Hemsworth et al. (1982) found that group housing and boar exposure reduced significantly the interval from weaning to remating for multiparous compared with control sows (2.3 vs 10.0 d and 11.7 vs 16.5 d, respectively). Walton (1986) also reported that multiparous, but not primiparous sows are sensitive to boar exposure during lactation, resulting in more multiparous sows exhibiting estrus and ovulating earlier after weaning than first-litter sows.

Exposure of anestrus ewes to intact rams at the onset of the breeding season stimulated estrous cyclicity in most cases (Schinckel, 1954). Ewes associated with rams either by direct contact or a combination of auditory, olfactory and/or visual stimulation experienced estrus within 17 d of exposure (Watson and Radford, 1960). Ewes exposed to rams experienced a large and immediate increase of luteinizing hormone (LH) in serum (Chesworth and Tait, 1974). Interval between ram introduction and the beginning of the preovulatory LH surge was 27 ± 4 h in one study, with 50% of the teased ewes ovulating within 41 h (Oldham et al., 1978). However, the majority of the ewes did not

exhibit estrus at this ovulation (Schinckel, 1954; Chesworth and Tait, 1974). Chesworth and Tait (1974) proposed that peak secretion of LH may trigger the onset of the breeding season such that ewes exposed to rams begin cycling at the same time, thus leading to the synchronization of estrus.

Altered Suckling

Partial weaning (removing some piglets of the litter at different times) has been shown to induce estrus in lactating sows or decrease the interval from weaning to estrus. Duration and type (total separation vs physical separation of the litter from sows) of separation appear to affect the estrual response of sows although the timing of initiation of treatment does not appear to be as critical if treatments are begun at a minimum of 2 wk pp (Stevenson and Davis, 1984). Smith (1961) reported that 12-h litter separation was effective for inducing estrus in lactating sows, but not 8-h litter separation. Other experiments employing 12-h litter separation failed to induce estrus during lactation (Crighton, 1970; Cole et al., 1972).

In some studies, piglets were partitioned alongside sows to prevent physical contact between the sow and litter (Thompson et al., 1981; Kirkwood et al., 1983). However, sows were still within visual, olfactory, and auditory range of their litters. According to Stolba and Henderson (1984), close proximity of sows to their piglets was likely to inhibit estrus during lactation. Perhaps close proximity between these sows and litters explains partially the reduced response (12.5 to 30.7% in estrus during lactation).

Periods of litter separation for 6 h were as effective as 12-h periods for

inducing lactational estrus in some studies (Walker and England, 1977; Stevenson and Davis, 1984). Grinwich and McKay (1985) reported that two 1-h daily nursing periods induced estrus during lactation in more multiparous than primiparous sows (85 vs 60%).

Reducing litter size (split weaning) 2 to 5 d before weaning resulted in earlier postweaning returns to estrus or an increase in the proportion of sows in estrus at various postweaning intervals (Stevenson and Britt, 1981; Britt and Levis, 1982; Cox et al., 1983a). Altering litter size before weaning such that sows nursed smaller litters (3 to 4 piglets) during 5 d before weaning resulted in fewer days from weaning to estrus for this group (Stevenson and Britt, 1981; Stevenson and Davis, 1984) as well as decreased duration of estrus (Stevenson and Britt, 1981). In general, multiparous sows are more sensitive to treatments imposed during lactation because more show estrus during lactation as well as have shorter intervals from weaning to estrus than primiparous sows (Stevenson and Davis, 1984; Grinwich and McKay, 1985).

Season and Parity

Parity and season influence the interval from weaning to remating in sows. An increase in this interval was observed in primiparous compared with multiparous sows in numerous studies (Rasbech, 1969; Aumaitre et al., 1976; King, 1978; Fahmy et al., 1979; Hurtgen et al., 1980; Karlberg, 1980; Benjaminsen and Karlberg, 1981; Szarek et al., 1981; Hemsworth et al., 1982). However, litter size increased with the age of dam at farrowing and parity had no direct effect on litter size of dams of the same age (French et al.,

1979). This suggests that reproductive performance of sows after weaning is probably influenced by age, not parity. Maclean (1969) and Brooks and Cole (1970) suggested that poor body condition following weaning may be responsible for the higher incidence of anestrus in primiparous sows. However, Stevenson and Davis (1984) and Esbenschade et al. (1986) found no significant relationship between changes in body condition and rebreeding performance of sows.

Hurtgen (1976) reported that the proportion of sows unmated by 30 d after weaning was higher on some swine farms in the U.S. during August, September, and October, whereas Szarek et al. (1981) reported the interval to conception to be longer during June through September. Similarly, Karlberg (1980) and Benjaminsen and Karlberg (1981) found the interval from weaning to estrus to be greater for primiparous sows in Norway from July through December. Whether this is an effect of temperature and/or photoperiod is unknown because the factors were confounded. However, it is known that in wild pigs, anestrus extends after weaning in late summer through December (Claus and Weiler, 1985).

Long photoperiods (16 to 24 h light) prolonged manifestations of behavioral estrus in sows (Perera and Hacker, 1984) and rats (Evans, 1981). In some studies, increased light resulted in increased milk production and weaning weight, survival rate and number of pigs weaned (Mabry et al., 1982a,b; Stevenson et al., 1983). Mabry et al. (1982b) suggested that photoperiod acts directly on piglets to promote growth or stimulate suckling behavior, thus resulting in improved sow and litter performance. In addition, whereas increasing light may improve synchrony of estrus after weaning (Stevenson et

al., 1983), days from weaning to estrus were not affected (Mabry et al., 1982b; Stevenson et al., 1983; Perera and Hacker, 1984). A recent study reported that temperature rather than season increased the weaning to remating interval in sows (Hemsworth et al., 1982). However, Hurtgen et al. (1980) suggested that delayed estrus after weaning was not due solely to higher temperatures during summer because longest intervals from weaning to estrus did not occur consistently during the hottest months, but occurred even when sows were in artificially cooled environments.

Nutrition

Nutrition appears to play an important role for reproductive function of sows. Type of feed and feed intake during gestation (O'Grady, 1967; Young and King, 1981), lysine intake during lactation (O'Grady and Hanrahan, 1975), protein intake during gestation and lactation (Svajgr et al., 1972) and postweaning feed intake (Brooks and Cole, 1972) all have an effect on the interval from weaning to estrus. Rowlinson and Bryant (1982a) reported that more sows exhibited estrus during lactation when grouped together, exposed to boars, and fed ad libitum. However, the response rate for ad libitum compared with restricted feeding was similar (28 vs 21%, respectively). Furthermore, Rowlinson and Bryant (1982b) found the incidence of lactational estrus to be similar for sows fed to appetite or to requirement, whereas both treatments had a higher response rate than sows fed 70% of their feed requirements.

Several studies have reported that energy intake during lactation had no effect on the number of days from weaning to first estrus in sows fed levels of

energy that met or exceeded the NRC (1979) recommendations for lactating sows (Elsley et al., 1968; O'Grady et al., 1973; Adam and Shearer, 1975). However, in more recent studies, interval from weaning to estrus in primiparous sows was reduced when energy or feed intake was increased during lactation (Hughes and Calder, 1979; Reese et al., 1980, 1981). Cox et al. (1983a) found that in summer, fat-supplemented diets reduced the interval from weaning to estrus in primiparous sows and increased the percentage of primiparous sows in estrus by 10 d postweaning. Furthermore, Reese et al. (1982) showed that the interval from weaning to estrus was increased in primiparous sows receiving low (8 Mcal) compared with high (16 Mcal) levels of metabolizable energy in lactational diets. In addition, sows that had large losses of weight and backfat during lactation experienced increased incidence of delayed estrus following weaning compared with those sows that maintained their body weight and backfat.

Prewaning Endocrine Traits of Sows

Ovarian Follicular Development

Trends in follicular development for sows during lactation have been reported. After parturition through the first week of lactation, a high proportion of atretic follicles are found on the ovaries (Palmer et al., 1965 a,b; Crighton and Lamming, 1969; Kunavongkrit et al., 1982). However, Kunavongkrit et al. (1982) reported equal numbers of normal and atretic follicles on d 14, 21 and 28 of lactation in primiparous sows, with more normal than atretic follicles on d 42 and 56 of lactation. Before weaning, most follicles are less than 5 mm

in diameter (Crighton and Lamming, 1969). Interestingly, primiparous sows have been reported to have smaller follicles prior to weaning than multiparous sows (2.00 to 4.99 vs 5 or more mm, respectively), although neither have follicles that reach ovulatory size prior to weaning (Palmer et al., 1965a; Kunavongkrit et al., 1982). Kunavongkrit et al. (1982) also reported an increase in the number of follicles on the ovaries as lactation progressed.

Preweaning Concentrations of FSH, LH and Prolactin

Lactational anestrus in the sow is characterized by a suppression of ovarian follicular growth and is associated with low content of luteinizing hormone (LH) and high content of follicle-stimulating hormone (FSH) in the anterior pituitary (Lauderdale et al., 1965; Palmer et al., 1965a; Crighton and Lamming, 1969). Concentrations of LH in serum are low in early lactation but undergo a slight but significant increase during progressive weeks of lactation (Parvizi et al., 1976; Stevenson and Britt, 1980; Stevenson et al., 1981; Kunavongkrit, 1984). Luteinizing hormone is secreted in episodic pulses in some sows during lactation with detectable pulses occurring approximately every 2 to 5 h (Edwards and Foxcroft, 1983; Shaw and Foxcroft, 1985). Concentrations of LH during lactation do not normally reach the level necessary for stimulation of ovulatory-size follicles (Crighton and Lamming, 1969; Stevenson and Britt, 1980; Duggan et al., 1982). Kunavongkrit (1984) reported that levels of LH during lactation were affected by number of nursing piglets, with sows nursing small (2 to 4 piglets) litters having higher LH than sows nursing larger (7 to 12 piglets) litters. Concentrations of FSH are low early in lactation but increase as

lactation progresses (Stevenson et al., 1981; Duggan et al., 1982).

Prolactin (PRL) rises approximately 1 wk prepartum with maximal levels observed around parturition (Benjaminsen, 1981b). During lactation PRL fluctuated widely, with concentrations peaking during suckling periods and declining during nonsuckling periods (Threfall et al., 1974; Landeghem and van de Wiel, 1978; Smith and Wagner, 1985). Stevenson et al. (1981) reported that PRL in serum decreased during 4 h when sow and litter were separated from each other, whereas a 5-fold increase in PRL was observed within 15 min after litter replacement.

Control of ovarian follicular development during and after lactation is dependent on gonadotropin secretion by the anterior pituitary. Stevenson et al. (1981) reported that FSH, but not LH increased after lactating sows were ovariectomized between 1 and 4 d pp, even though total estrogens in serum were unchanged. They suggested that secretion of FSH may be controlled by inhibin, whereas LH secretion was inhibited by the suckling stimuli of the litter, probably through neural inhibition of GnRH from the hypothalamus. Increases in concentrations of LH and FSH as lactation progressed may be associated with the natural reduction in the suckling frequency of the litter (Niwa et al., 1951).

Response of LH to estradiol changes progressively with weeks of lactation, with no increase in secretion of LH early in lactation after an injection of estradiol benzoate, but with significant increases in LH after estradiol by 3 to 4 wk of lactation (Elsaesser and Parvizi, 1980; Ramirez et al., 1985). Therefore, a positive feedback response of LH to estradiol appears to be lacking in the early pp period. Bevers et al. (1981) reported that the LH

response to synthetic GnRH increases from the first to the second and the second to the third week of lactation, whereas the reverse was observed by Stevenson et al. (1981). Presence or absence of litters did not change the response of LH to GnRH even though concentrations of PRL in serum were much greater when the litter was present. When sows were treated with bromocriptine (ergot alkaloid) to decrease concentrations of PRL in serum, the LH response to GnRH was unchanged. Therefore, PRL may not play a role in the suckling-induced suppression of LH secretion or in the lower LH response to GnRH early in lactation (Britt et al., 1985).

Duggan et al. (1982) reported that sows grouped with their litters and a boar 18 d pp showed an increase in concentrations of LH in plasma. Although all sows in this group exhibited lactational estrus, only one farrowed to service during this period. They concluded that failure to conceive during lactation was probably due to the absence or impairment of ovulation, as suggested by abnormal concentrations of progesterone (P) in plasma.

Secretion of Estradiol, Progesterone and Corticosteroids Before Weaning

Concentrations of P in serum of pregnant sows began to decline 5 d prepartum (Molokwu and Wagner, 1973; Baldwin and Stabenfeldt, 1975), fell dramatically 2 d before parturition (Edqvist et al., 1974; Ash and Heap, 1975; Baldwin and Stabenfeldt, 1975; Duggan et al., 1982), and reached basal levels by 24 h pp (Molokwu and Wagner, 1973; Edqvist et al., 1974; Baldwin and Stabenfeldt, 1975). Concentrations of P remained low throughout lactation (Ash and Heap, 1975; Baldwin and Stabenfeldt, 1975; Stevenson et al., 1981;

Kunavongkrit et al., 1982).

Estrogens increased markedly to maximal levels 2 d prepartum, decreased after the onset of parturition, and remained low throughout lactation (Molokwu and Wagner, 1973; Edqvist et al., 1974; Ash and Heap, 1975; Baldwin and Stabenfeldt, 1975; Holness and Hunter, 1975; Stevenson et al., 1981; Duggan et al., 1982). Holness and Hunter (1975) suggested that the pp or farrowing estrus of sows is a result of the peak of feto-placental estrogens that occurred at parturition. This conclusion was reached when a sow ovariectomized d 108 of gestation exhibited pp estrus.

Corticosteroids are highly variable in sows with elevated concentrations occurring both the day before and the day after parturition, whereas peak levels were observed on the day of farrowing (Molokwu and Wagner, 1973; Baldwin and Stabenfeldt, 1975). Concentrations of corticosteroids in plasma during lactation were slightly lower than those observed during pregnancy (Ash and Heap, 1975). Kunavongkrit et al. (1984) reported that levels of cortisol in plasma were higher in both lactating and anovulatory zero-weaned (weaned by 12 h pp) sows than in ovulatory zero-weaned sows. Also, concentrations of cortisol were similar for sows nursing small or average-size litters. Elevated levels of cortisol therefore may contribute to the inhibition of LH secretion or the LH surge during the first estrus after zero weaning or promote anestrus in lactating sows.

Postweaning Endocrine Traits of Sows

Changes in FSH, LH and Prolactin After Weaning

Removing piglets from sows at weaning resulted in marked changes in hormonal secretion with duration of lactation affecting patterns of secretion. Removal of the suckling pigs resulted in a dramatic decrease in concentrations of PRL in serum within 1 to 2 h (van Landeghem and van de Wiel, 1978; Benjaminsen, 1981b; Edwards and Foxcroft, 1983; Kirkwood et al., 1984; Shaw and Foxcroft, 1985). Concentrations of LH increased immediately after weaning (Crighton and Lamming, 1969; Aherne et al., 1976; Stevenson and Britt, 1980; Stevenson et al., 1981; Edwards and Foxcroft, 1983; Shaw and Foxcroft, 1985) with increased frequency of LH pulses evident 2 to 3 d postweaning (Cox and Britt, 1982b; Shaw and Foxcroft, 1985). Concentrations of LH preweaning were related inversely to the interval from weaning to estrus (Shaw and Foxcroft, 1985). Concentrations of FSH increased after weaning (Edwards and Foxcroft, 1983; Shaw and Foxcroft, 1985), but the increase was not as great as for LH, nor was there a definite episodic pattern of FSH release (Britt et al., 1985).

Sows weaned 10 d after farrowing had lower lactational and postweaning levels of LH in plasma than sows weaned after 35 d (Kirkwood et al., 1984). In addition, pattern of LH secretion was altered, as evidenced by an attenuated preovulatory LH surge of less magnitude than that for sows weaned later in lactation. Edwards and Foxcroft (1983) similarly found that shorter periods of lactation reduced the preovulatory LH surge and altered the pattern of FSH release. A correlation between ovulation rate and peak concentrations of the rise in FSH after weaning also was suggested (Shaw and Foxcroft, 1985).

Secretion of Estradiol, Progesterone and Corticosteroids After Weaning

Stevenson and Britt (1980) reported that estrogens in serum rose slightly between weaning and estrus, peaked 24 h around the onset of estrus prior to the preovulatory surge of LH and FSH (Ash and Heap, 1975; Aherne et al., 1976; Stevenson et al., 1981), and declined after onset of estrus. Progesterone may increase transiently at weaning, decline until estrus and rise about 30 h after the preovulatory LH surge (Stevenson and Britt, 1980; Shaw and Foxcroft, 1985). Corticosteroids remained low in plasma after weaning until just prior to estrus, when a dramatic increase in concentration was observed (Ash and Heap, 1975).

A relationship between adrenal and reproductive function has been demonstrated in pigs. Injections of adrenocorticotropin hormone (ACTH) blocked ovulation, delayed estrus and was associated with a high incidence of ovarian cysts in sows (Liptrap, 1970; Barb et al., 1982). Schilling and von Rechenberg (1973) reported that treatment with ACTH or flumethasone to increase concentrations of cortisol blocked ovulation in gilts. This effect could be overcome partly by treatment with hCG, suggesting that LH secretion may have been altered by ACTH. Therefore, hypersecretion of ACTH due to stressful stimuli could suppress the preovulatory surge of LH, block ovulation and alter normal reproduction in sows.

Concentrations of Insulin and Thyroxine in Serum of Sows

The effects of insulin on sow reproductive performance are relatively unknown. Uvnas-Moberg et al. (1984) reported that insulin increased in lactating sows approximately 100% for 10 min in response to a suckling stimulus by piglets and that feeding influenced insulin secretion in a similar manner as

suckling. Secretion of insulin in response to suckling may be due to reflex activation of the vagal nerves that cause a release of insulin (Uvnas-Moberg and Eriksson, 1983). Large litters and longer suckling periods were related to increases in insulin secretion (Uvnas-Moberg et al., 1984). Insulin has been shown to stimulate synthesis of casein and lactalbumin in mouse mammary epithelial cells, and might therefore promote milk production in some species (Bolander et al., 1981). High circulating levels of insulin are associated with a decreased capacity for milk production in cows (Bines and Hart, 1982).

The role of thyroxine (T₄) in sow reproduction also remains obscure. Nachreiner (1972a,b) reported that levels of T₄ in the pregnant sow were lower 3 mo after conception and around parturition than earlier in gestation. In addition, both triiodothyronine and T₄ were increased significantly 24 h after parturition when compared with levels in the prepartum period. A more recent study found that levels of T₄ decreased during the last trimester of gestation, reached a nadir at the time of farrowing and remained low during lactation (Benjaminsen, 1981b). Benjaminsen (1981b) found a negative correlation between the number of suckling piglets and preweaning concentrations of T₄. Levels of T₄ increased rapidly during the 2-wk period after weaning and was not different for sows in estrus early (by 6 d) or late (19 d) postweaning (Benjaminsen, 1981b). Thyroid function influences reproduction in women with hyperthyroidism being highly correlated with ovulation failure and increased incidences of spontaneous abortion (Potter, 1980). Ovulation without estrus in the cow also has been associated with thyroidectomy or hypothyroidism (Wilson, 1975).

Reese (1983) suggested from preliminary data that the delayed return to

estrus of primiparous sows fed restricted energy during lactation was caused by hyperthyroidism. Mean concentrations of T4 in serum for anestrus sows were higher than those observed for normal cyclic sows. In further studies, however, Nelssen (1983) reported that sows offered restricted energy during lactation and failed to return to estrus after weaning tended to be hypothyroid.

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Duration of litter separation and boar exposure influences oestrous
expression of sows during and after lactation

Summary. Effect of litter separation (LS), boar exposure (BE), and parity on oestrous expression by sows during lactation was studied in 3 experiments using a total of 112 crossbred sows. In Experiment 1 (October and December, 1983), limiting duration of LS (3 vs 6 h) did not preclude expression of oestrus during lactation when BE was provided. Prewaning interval to oestrus was less for multiparous than primiparous sows and more multiparous than primiparous sows were in oestrus during lactation. Litter separation and/or BE failed to induce oestrus during lactation in either primiparous or multiparous sows during August, 1985 (Experiment 2). In Experiment 3 (October and November, 1985), more LS than nonLS sows exhibited oestrus during lactation, whereas LS and/or BE had no effect on intervals to postweaning oestrus. These data suggest that multiparous sows are more responsive to treatment during lactation than primiparous sows, resulting in more multiparous sows in oestrus during lactation and shorter intervals to oestrus postweaning than for primiparous sows. Litter separation appeared to be more essential for inducing lactational oestrus than BE when no LS was provided.

Introduction

Recent studies have shown that lactational oestrus or shorter postweaning intervals to oestrus can be induced in sows when suckling is altered or disrupted. Grouping sows and their piglets at 2 to 3 weeks postpartum in the

presence (Petchey & Jolly, 1979; Rowlinson & Bryant, 1981; Duggan, Bryant & Cunningham, 1982; Rowlinson & Bryant, 1982) or absence (Smith, 1961) of a boar resulted in oestrus and(or) fertile matings during lactation. In some studies, sows grouped with their litters, but not exposed to boars (Bryant, Palmer, Petherick & Rowlinson, 1983), exhibited oestrus much less frequently (3.0 vs 78.3%) than sows grouped together, exposed to boars, and fed ad libitum (Rowlinson & Bryant, 1976; Petchey, Dodsworth & English, 1978; Bryant & Rowlinson, 1984). Sow and litter separation (6 or 12 h/day) induced oestrus during lactation when boar exposure was provided (Walker & England, 1977; Stevenson & Davis, 1984). Petchey & English (1980) and Hemsworth, Salden & Hoogerbrugge (1982) found that group housing of sows and boar exposure during lactation reduced the interval from weaning to remating for those multiparous sows that did not exhibit oestrus during lactation. The objectives of the present studies were to 1) examine further the effect of duration of litter separation and boar exposure on oestrous response of sows during lactation; 2) partition the effects of litter separation from boar exposure on oestrous expression by sows during lactation; and 3) determine the influence of parity on oestrous response to altered suckling and boar exposure.

Materials and Methods

Exp. 1. Two trials were conducted in October and December 1983 with 39 crossbred (Yorkshire x Duroc) sows of mixed parity. Sows were assigned randomly within parity (primiparous vs multiparous) to two treatment groups (no control). Treatment consisted of separating sows from their litters for 3 (n=20)

or 6 (n=19) h/day plus boar exposure for 1 h/day (LS + BE) beginning 8 days before weaning piglets from sows at 3 to 4 weeks (19 to 31 days) of age. When possible, the number of nursing piglets was standardized to 6-10 pigs within 48 h post partum. Sows were fed ad libitum a diet consisting of milo and soybean meal (14% protein) balanced for protein and energy, plus supplemental vitamins, minerals, and salt to meet NRC (1979) requirements for lactating sows. Body weights of sows 1 day after farrowing and at weaning were measured to determine treatment effects on weight loss during lactation. Sows were confined to farrowing crates during lactation except during periods of treatment. When sows were separated from their litters, they were moved from their farrowing crates to adjacent outside pens, exposed to a mature boar, and observed for estrus during the first hour of separation.

Data were analyzed by least-squares analysis of variance using the General Linear Models procedure of the Statistical Analysis System (SAS, 1979). Trial (N=2), treatment (N=2), and parity (primiparous vs multiparous) plus all two-way interactions were evaluated in initial models. No significant trial or treatment x trial interactions were detected, so trial was eliminated in further analyses. Other characteristics (days to oestrus from LS + BE and from weaning, and sow weight at weaning) also were analyzed similarly with treatment (N=2) and parity (N=2) plus two-way interactions as sources of variation. Comparisons among treatment means were made by Scheffe's interval (Gill, 1978).

Exp. 2. Experiment 2 was conducted in August, 1985 with 27 crossbred (50% Yorkshire x Duroc; 50% Chester White) sows of mixed parity. Sows were assigned randomly within parity to four treatment groups (2 x 2 factorial experiment). Treatments consisted of 1) separating sows from their litters (LS)

for 6 h/day plus boar exposure (BE) for 1 h/day (LS + BE), 2) LS + no BE (LS + NBE), 3) no LS + BE (NLS + BE), and 4) no LS + no BE (NLS + NBE) or controls. Treatments began 8 days before weaning. Sows were fed and housed in farrowing crates as described in Exp. 1 except during periods of treatment. Sows in the LS + NBE groups were moved to outside pens (with concrete floors) at 0600 h and returned to their litters at 1200 h. Sows were checked for signs of oestrus by the same individual during the first hour of separation. Since no boar contact was allowed for this group, sows were considered oestrous when they stood to be mounted by other sows or responded positively to back pressure. Sows in the LS + BE group were moved (1200 h) to the same outside pens occupied previously by the LS + NBE sows. A mature boar was introduced to the LS + BE group from 1215-1315 h and sows were observed for signs of oestrus. At 1800 h sows were returned to their litters and outside pens were scraped, washed, and allowed to dry overnight. Sows in the BE + NLS group were housed in raised farrowing crates in a room separate from the other treatment groups. A boar was brought to the room and allowed access to the sows at the front of each crate only. Care was taken to ensure that the boar approached the front of each crate at least four times during BE (1230-1330 h). Control sows were neither separated from their litters nor exposed to boars until after weaning. All sows were exposed to boars for oestrous detection after weaning.

Piglets were weaned from sows at 4 weeks of age. Feed intake of sows during the experiment, and weight of sows and litters at weaning were recorded to determine the influence of litter separation and/or boar exposure on weight loss of sows, growth of litters during lactation, and feed intake of the sows for

the duration of treatment.

Data were analyzed by least-squares analysis of variance as described for Exp. 1. Treatment (N=4) and parity (primiparous vs multiparous) plus all two-way interactions were evaluated in the models. Pre-planned orthogonal contrasts were made to compare main effects: LS vs NLS, and BE vs NBE. Other traits (days to oestrus, sow weight, litter weight, and sow feed intake) were analyzed similarly with treatment (N=4) and parity (N=2) plus two-way interactions as sources of variation. Further comparisons of means were by Scheffe's interval (Gill, 1978).

Exp. 3. Two trials were conducted in October and November, 1985 with design and procedures similar to those described in Exp. 2. However, in this experiment, only primiparous sows were utilized and piglets were weaned from sows at 3 weeks of age. Data were analyzed by least-squares analysis of variance as described for Exp. 2. Treatment (N=4) and trial (N=2) plus all two-way interactions were evaluated in initial models. No significant trial or treatment x trial interactions were detected, so trial was eliminated from further analyses. Pre-planned orthogonal contrasts were made to compare main effects: LS vs NLS, and BE vs NBE. Other traits (days to oestrus, sow weight, litter weight, and sow feed intake) were analyzed similarly with treatment (N=4) as a source of variation. Further comparisons of means were by Scheffe's interval (Gill, 1978).

Results

Exp. 1. Table 1 illustrates the similarities of litter size, sow weights, lactation

lengths at the onset of treatments, and the number of sows in the 3- or 6-h LS + BE treatment and parity groups. Oestrous expression during lactation (preweaning) or after weaning (postweaning) for sows in the 3- or 6-h treatment (LS + BE) and parity groups are illustrated in Fig. 1. Percentage of sows in oestrus preweaning was similar for the 3 (65%) and 6-h (79%) treatments. However, more ($P<0.05$) multiparous (88%) than primiparous (38%) sows were in oestrus preweaning (Fig. 1).

Intervals to oestrus for sows expressing oestrus preweaning and postweaning are in Table 2. Whereas preweaning intervals to oestrus tended to be less ($P<0.10$) for 6 than 3-h LS + BE sows, postweaning intervals were similar. Multiparous sows returned to oestrus during lactation slightly but not significantly earlier than primiparous sows, and postweaning intervals to oestrus were shorter ($P<0.05$) for multiparous than primiparous sows.

Exp. 2. Table 3 illustrates that length of lactation, sow weight at weaning, litter size, and litter weight were similar among treatment groups (August trial). However, sows that were NLS + BE consumed more feed ($P<0.05$) during the treatment period than the remaining sows. Furthermore, multiparous sows consumed more ($P<0.05$) feed than primiparous sows as expected.

No sows in this August trial expressed oestrus during lactation (Table 4). This absence of lactational oestrus was true for both parity groups. Whereas no treatment effects were obvious for postweaning intervals to oestrus, sows that were BE + NLS tended ($P<0.10$) to have shorter intervals from weaning to oestrus than those of controls (NBE + NLS). Multiparous sows tended to return to oestrus after weaning sooner than primiparous sows (Table 4).

Exp. 3. Length of lactation, litter size, and feed intake of sows were

similar for treatment groups (Table 5) in the October and November trials. However, control (NBE + NLS) sows weighed more ($P < 0.05$) at weaning than the NBE + LS sows, but neither group was different in weight from BE sows that were either LS or NLS. Control sows also had lighter ($P < 0.05$) litters than the BE + NLS and NBE + LS sows, but had similar litter weights as the BE + LS treatment group.

Only sows that were LS came into oestrus during lactation (Fig. 2). More LS than nonLS sows (8/26 vs 0/20) were in oestrus during lactation, regardless of BE (i.e., 3 sows were NBE and 5 were BE). For sows that were in oestrus preweaning, intervals to oestrus were similar (Table 6). Intervals to postweaning oestrus were unaffected by LS and/or BE, although they tended to be less for sows receiving BE without LS.

Discussion

These studies have provided new information about factors involved in removing the inhibition of suckling on reproductive function during and after lactation in sows. Our experiments were designed to address several concepts concerning the influence of 1) concomittant altered suckling and boar exposure; 2) duration of altered suckling; and 3) season and parity on reproductive quiescence that is normally associated with lactation in sows.

As long as sows were exposed to boars for at least 1 h/day, neither 3- (65%) nor 6- (79%) h LS increased the proportion of sows in oestrus during lactation. In our earlier studies, when 6- and 12-h LS were compared, similar conclusions were made (Stevenson & Davis, 1984). Apparently, abrupt changes in

patterns of suckling can induce oestrus in sows, as others have demonstrated when duration of separation has varied from 6 to 22 h (Smith, 1961; Walker & England, 1977; Thompson, Hanford & Jensen, 1981; Grinwich & McKay, 1985). These data combined suggest that a minimal duration of LS may initiate events leading to oestrus during lactation. If there is any advantage for increased duration of LS on oestrous cyclicity, our present data suggest that 6-h LS tended to reduce the interval to oestrous expression in sows that came into oestrus during lactation compared with 3-h LS (Table 2).

Our data provide evidence that the factors of LS and BE may be additive. Litter separation proved to be more critical for initiation of oestrous cyclicity during lactation than BE without LS. Only LS sows expressed oestrus, of which 5 were BE and 3 were NBE. The fact that few sows came into oestrus during lactation without LS even though they were exposed to boars (Walton, 1986), suggests the importance of first reducing the inhibition of suckling on gonadotropin secretion (Henderson & Hughes, 1984) and then initiating gonadotropin release by providing BE. This has been demonstrated by providing BE to prepubertal gilts (Brooks & Cole, 1970; Mavrogenis & Robison, 1976) and ram exposure to seasonally anoestrous ewes (Chesworth & Tait, 1974; Oldham, Martin & Knight, 1978; Walton, McNeilly, McNeilly & Cunningham, 1978).

Rowlinson & Bryant (1982) reported that occurrence of lactational oestrus was highest for sows grouped with other sows and their litters, exposed to boars, and fed ad libitum beginning 20 days post partum. Grouping of sows and providing BE initiated oestrus in a higher proportion of sows compared with those not grouped nor BE, whereas additional feed availability was without effect. Rowlinson & Bryant (1982) suggested a synergism for the three factors

they examined, all being necessary to maximize the incidence of lactational oestrus in sows.

It is equally interesting in all studies for which data were reported that sows failing to respond to altered suckling, BE, and(or) increased feed availability during lactation, expressed oestrus after weaning at intervals similar to nontreated herdmates (Rowlinson & Bryant, 1982; Stevenson & Davis, 1984). Prewaning exposure of sows to boars failed to reduce the interval from weaning to oestrus in several studies (Petchey & English, 1980; Hemsworth et al., 1982; Walton, 1986). We suggested earlier that the oestrous response to treatment during lactation may be an "all-or-none" phenomenon because sows failing to respond to LS and(or) BE before weaning have normal rather than intermediate intervals to oestrus after weaning (Stevenson & Davis, 1984). The exception to this statement is exemplified by studies in which treatments of altered suckling occurred during the last 48 to 120 h of lactation reduced postweaning intervals to oestrus. These treatments, however, were administered too late in lactation to allow an oestrous response to occur during lactation (Stevenson & Britt, 1981; Britt & Levis, 1982; Stevenson & Davis, 1984).

The influence of parity in Exp. 1 and 2 was quite distinct. Multiparous sows in all treatments tended to return to oestrus sooner after weaning and proportionally more multiparous sows exhibited lactational oestrus than primiparous sows. Similarly, Stevenson & Davis (1984) and Walton (1986) reported that multiparous sows returned to oestrus after weaning earlier than primiparous sows.

Influence of season on oestrous expression of sows during lactation has not been reported previously. It appeared that increased photoperiod and(or)

temperature associated with summer inhibited response to LS and/or BE in the August experiment. Interestingly, postweaning intervals to oestrus during August were not prolonged for either multiparous or primiparous sows in any of the treatments, conflicting with other reports in which season lengthened postweaning intervals to oestrus (Hurtgen, 1976; Karlberg, 1980; Benjaminsen & Karlberg, 1981; Szarek, Levis & Britt, 1981), especially for primiparous sows. Perhaps LS and/or BE reduced the suckling inhibition on reproductive function sufficient to over-ride the detrimental effects of season on prolonged postweaning intervals to oestrus in our studies. However, as control sows in August returned to oestrus in a manner similar to treated animals, LS and/or BE cannot account totally for this response.

Our studies demonstrated that duration of LS is not critical for our sows to exhibit oestrus during lactation, whereas some disruption of the suckling pattern during lactation is essential for exhibiting lactational oestrus. Boar exposure appeared to be an additive factor to LS for inducing lactational oestrus, however, BE alone did not induce oestrous cyclicity in lactating sows. Parity and seasonal effects on lactational oestrus were demonstrated. Multiparous sows were more responsive to treatment than primiparous sows during lactation, whereas sows of either parity seemed to lose their ability to respond to LS and(or) BE during August.

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Table 1. Effects of duration of litter separation (LS), boar exposure (BE) and parity on sow performance (Exp. 1)

Item	No. of sows	Days post partum	Sow weight at weaning (kg)	Litter size (piglets/sow)
Treatment				
3 h LS + 1 h BE	20	18.7 ± 3.1	186.9 ± 6.6	7.8 ± 0.4
6 h LS + 1 h BE	19	19.0 ± 2.4	182.9 ± 7.6	7.6 ± 0.5
Parity				
Primiparous	13	17.9 ± 3.6	153.1 ± 7.3 ^a	8.2 ± 0.5
Multiparous	26	19.4 ± 2.9	216.7 ± 7.9 ^b	7.3 ± 0.5

^{a,b} Means with different superscripts differ ($P < 0.05$).

Fig. 1. Influence of litter separation and boar exposure (LS + BE) and parity on the percentage of sows in oestrus pre- and postweaning (Exp. 1).

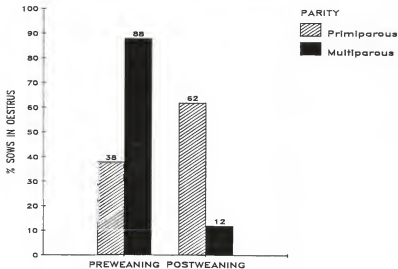
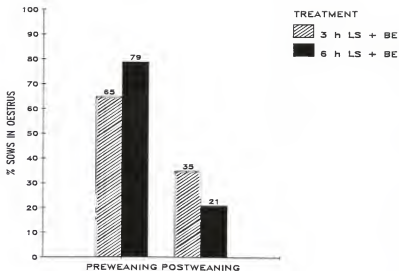


Table 2. Effects of duration of litter separation (LS), boar exposure (BE), and parity on days to oestrus pre- and post weaning (Exp.1)

Item	No. of sows	Days to oestrus	
		Prewaning*	Postweaning
Treatment			
3 h LS + 1 h BE	20	5.7 ± 0.4 (13)**	5.4 ± 2.0 (7)
6 h LS + 1 h BE	19	4.8 ± 0.3 (15)	5.7 ± 1.7 (4)
Parity			
Primiparous	13	5.6 ± 1.5 (5)	6.0 ± 1.8 ^a (8)
Multiparous	26	4.6 ± 0.8 (23)	3.7 ± 0.6 ^b (3)

a,b Means within item having different superscripts differ ($P < 0.05$).

*Denotes sows manifesting oestrus during lactation.

**Number of sows.

Table 3. Effects of boar exposure (BE), litter separation (LS), BE + LS, and parity on sow and litter performance (Exp. 2).

Item	No. of sows	Days post partum	Sow weight at weaning (kg)	Litter size (piglets/sow)	Litter weight at weaning (kg)	Daily sow feed intake (kg)
Treatment						
BE + NLS	7	18.9 ± 1.7	170.7 ± 5.6	8.1 ± 1.5	51.1 ± 3.7	6.3 ± .3 ^a
NBE + LS	8	17.9 ± 1.6	162.1 ± 6.2	7.7 ± 1.6	47.6 ± 4.1	4.9 ± .3 ^b
BE + LS	8	20.1 ± 2.0	164.8 ± 6.1	8.0 ± 1.4	46.7 ± 4.0	4.8 ± .3 ^b
NBE + NLS	4	18.7 ± 1.9	178.4 ± 7.6	7.7 ± 1.7	45.1 ± 5.0	5.0 ± .4 ^b
Parity						
Primiparous	10	17.7 ± 1.6	144.0 ± 5.3 ^a	7.9 ± 1.5	43.8 ± 3.5	4.9 ± .3 ^a
Multiparous	17	19.7 ± 1.9	194.0 ± 4.3 ^b	7.9 ± 1.4	49.5 ± 2.9	5.8 ± .2 ^b

^{a, b} Means with different superscripts differ ($P < 0.05$).

Table 4. Effects of boar exposure (BE), litter separation (LS), LS + BE, and parity on days to oestrus pre- and post weaning (Exp.2)

Item	No. of sows	Days to oestrus	
		Preweaning*	Postweaning
Treatment			
BE + NLS	7	— (0)**	4.6 ± 0.6 (7)
NBE + LS	8	— (0)	5.0 ± 0.5 (8)
BE + LS	8	— (0)	5.1 ± 0.5 (8)
NBE + NLS	4	— (0)	6.0 ± 0.7 (4)
Parity			
Primiparous	10	— (0)	5.5 ± 0.5 (10)
Multiparous	17	— (0)	4.8 ± 0.4 (17)

*Denotes sows manifesting oestrus during lactation.

**Number of sows.

Table 5. Effects of boar exposure (BE), litter separation (LS), and BE + LS on sow and litter performance (Exp. 3).

Item	No. of sows	Days postpartum	Sow weight at weaning (kg)	Litter size (piglets/sow)	Litter weight at weaning (kg)	Daily sow feed intake (kg)
BE + NLS	12	15.3 ± 0.8	155.7 ± 2.9 ^{ab}	8.6 ± 0.3	41.6 ± 1.6 ^a	5.1 ± .3
NBE + LS	13	15.0 ± 0.8	149.3 ± 2.8 ^a	8.2 ± 0.3	40.4 ± 1.6 ^a	4.1 ± .3
BE + LS	13	13.4 ± 0.8	151.5 ± 2.8 ^{ab}	8.2 ± 0.3	35.0 ± 1.6 ^b	4.0 ± .3
NBE + NLS	8	12.5 ± 1.0	162.7 ± 3.5 ^b	7.3 ± 0.4	31.8 ± 2.0 ^b	4.6 ± .4

a,b Means with different superscripts differ ($P < 0.05$).

Fig. 2. Influence of litter separation and boar exposure (LS + BE) on the percentage of sows in oestrus pre- and postweaning (Exp. 3).

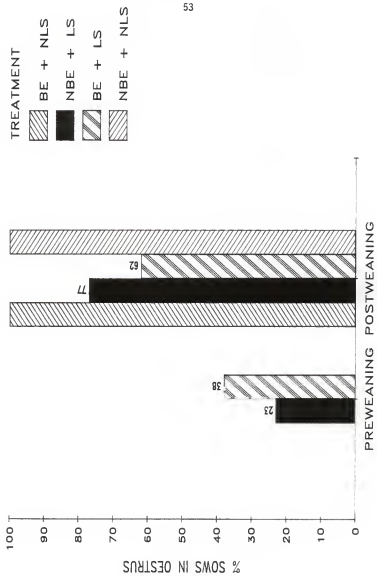


Table 6. Effects of boar exposure (BE), litter separation (LS), and BE + LS on days to oestrus pre- and post weaning (Exp. 3).

Item	No. of sows	Days to oestrus	
		Prewaning*	Postweaning
BE + NLS	12	- (0)**	4.1 \pm 0.3 (12)
NBE + LS	13	5.4 \pm 1.0 (3)	4.6 \pm 0.3 (10)
BE + LS	13	5.5 \pm 0.8 (5)	5.1 \pm 0.3 (8)
NBE + NLS	8	- (0)	4.7 \pm 0.3 (8)

*Denotes sows manifesting oestrus during lactation.

**Number of sows.

Endocrine Changes in Sows in Response to Altered Suckling and Boar Exposure

Summary. Eighteen sows (6 primiparous and 12 multiparous) were allotted randomly to two lactational treatments: litter separation (LS; 6 h/day) plus boar exposure (BE; 1 h/day; N=14) beginning 8 days before weaning and no LS + no BE (Controls; N=4). Blood was collected from all sows via indwelling vena cava catheters at 20-min intervals for 5 h on days -1, 0, 1, 2, and 3 from initiation of treatment. Control and LS + BE sows not exhibiting oestrus during lactation were sampled again on days -1, 0, 1, and 2 from weaning. All 10 multiparous sows in the LS + BE group (treated multiparous; TM) exhibited oestrus during lactation, whereas none of the 4 primiparous LS + BE (treated primiparous; TP) nor none of the 2 control multiparous (CM) and 2 control primiparous (CP) sows exhibited lactational oestrus. Overall and baseline concentrations of LH in serum were higher ($P<0.05$) in TM and TP sows than CM and CP sows during lactation, whereas overall FSH was higher ($P<0.05$) in primiparous (TP and CP) than multiparous (CM and TM) sows. Number of LH pulses was greater ($P<0.05$) for TP than TM sows during lactation. Insulin in serum was higher ($P<0.05$) in CM than TM sows, whereas thyroxine was unaffected. Oestradiol-17 β increased ($P<0.05$) during LS + BE and was higher ($P<0.01$) in TM than CM or CP sows. Prewaning cortisol and progesterone in serum were higher ($P<0.05$) in TM than CM sows, and in TP than CP sows.

Number of LH pulses was greater ($P<0.05$) in TP than CM or CP sows after weaning. Postweaning concentrations of FSH, insulin, and thyroxine in serum were unaffected by preweaning treatments. These data suggest that 1)

LS and BE increase basal LH and pulsatile secretion of LH and FSH in both multiparous and primiparous sows; 2) possible lack of ovarian follicular development and oestradiol secretion may preclude expression of oestrus in primiparous sows during lactation despite higher concentrations of FSH and LH in serum; and 3) elevated cortisol and progesterone in response to LS + BE may inhibit the onset of oestrous cycles in primiparous, but not multiparous sows during lactation.

Introduction

Lactating sows are normally considered to be both anoestrous (Burger, 1952) and infertile (Polge, 1972). Lactational anoestrus in sows is characterized by suppressed ovarian follicular growth, and low content of luteinizing hormone (LH) and high content of follicle-stimulating hormone (FSH) in the anterior pituitary (Lauderdale, Kirkpatrick, First, Hauser & Casida, 1965; Palmer, Teague & Venzke, 1965; Crighton & Lamming, 1969). Concentrations of LH and FSH in serum are low in early lactation but undergo slight (LH) to significant (FSH) increases during progressive weeks of lactation (Parvizi, Elsaesser, Smidt & Ellendorff, 1976; Stevenson & Britt, 1980; Stevenson, Cox & Britt, 1981; Duggan, Bryant & Cunningham, 1982; Kunavongkrit, 1984). Oestrogens and progesterone remain low throughout lactation (Ash & Heap, 1975; Baldwin & Stabenfeldt, 1975; Holness & Hunter, 1975; Stevenson et al., 1981; Duggan et al., 1982; Kunavongkrit, Einarsson & Settergren, 1982), whereas corticosteroids are higher during lactation than pregnancy (Molokwu & Wagner, 1973; Ash & Heap, 1975; Baldwin & Stabenfeldt, 1975; Kunavongkrit, Madej & Einarsson, 1984).

Duggan et al. (1982) attempted to characterize the endocrine response of sows that were grouped together with their litters and exposed to boars from approximately 16 days post partum. They reported increased plasma LH activity, whereas FSH was unaltered. Although all 5 sows group-housed and boar exposed exhibited oestrus during lactation, only one subsequently farrowed. Duggan et al. (1982) suggested that absence or impairment of ovulation, as determined by concentrations of progesterone in plasma, was responsible for reduced conception rates. The endocrine response of sows separated from their litters and exposed to boars during lactation has not been characterized. Our objectives were to examine this response, and to determine the influence of parity on endocrine changes associated with litter separation and boar exposure during lactation and after weaning.

Materials and Methods

Treatments and animal management

Twelve multiparous and 6 primiparous crossbred (Yorkshire X Duroc) sows were allotted randomly within parity to two treatments: litter separation (LS, 6 h/day) plus boar exposure (BE, 1 h/day; N=14) or no LS + no BE (N=4) beginning 8 days before weaning (4 weeks). Multiparous (M) and primiparous (P) sows in the LS + BE group were designated as treated (TM and TP) sows, whereas M (N=2) and P (N=2) sows not separated from their litters nor exposed to boars were designated as controls (CM and CP). Indwelling catheters were inserted nonsurgically (Ford & Maurer, 1978) into the vena cava of each sow 3 days before treatment was initiated at an average of 19 ± 1.9 days post partum. Number of nursing piglets was standardized to 7-10 piglets within 48 h post partum. Sows were fed a milo-soybean meal diet (14%

protein) balanced for protein and energy plus supplemental vitamins, minerals, and salt to meet NRC (1979) requirements for lactating sows. Sow and litter weights were recorded 1 day before treatment began and at weaning to determine treatment effects on weight changes during lactation. Sows were confined to farrowing crates during lactation except during periods of treatment. When sows were separated from their litters, they were moved (1000 h) from their farrowing crates to adjacent outside pens, exposed to a mature boar, and observed for oestrus during the first hour of separation. Sows were returned to their litters at 1600 h.

Scheme for blood collection

Blood was collected from sows at 20-min intervals from 1200 to 1700 h on days -1, 0, 1, 2, and 3 from treatment (i.e., sampling began 2 h after LS + BE and continued 1 h after sows were reunited with piglets). Control (2 CM and 2 CP) and 4 TP sows not detected in oestrus during lactation were subjected to a similar sampling regimen on days -1, 0, 1, and 2 from weaning. Blood was kept on ice following collection and then held at 5 C for 24 h until serum was obtained by centrifugation. Serum was frozen at -20 C until assayed. All individual serum samples (16/day) from 18 sows preweaning and 8 sows postweaning were radioimmunoassayed for LH and FSH, and sera from hourly samples (1200, 1300, 1400, 1500, 1600, and 1700 h) were assayed for insulin and thyroxine on days -1, 0, 1, and 2. Daily serum pools from each of the 18 sows preweaning (days -1, 0, 1, 2, and 3 from LS + BE) and 8 sows postweaning (days -1, 0, 1, and 2 from weaning) were radioimmunoassayed for oestradiol-17 β , progesterone, and cortisol.

Hormone assays

LH. Concentrations of LH in porcine serum (pLH) were determined by a double-antibody radioimmunoassay (RIA) similar to that described by Kraeling, Rampacek & Cox (1982) with modifications. Purified pLH (USDA-pLH-I-1, 2.5 µg) was reacted with 15 µg chloramine-T and 500 µCi ^{125}I . The reaction was stopped with 60 µg of sodium metabisulfite and ^{125}I -pLH was separated from free ^{125}I by anion exchange (AG 2 x 8, chloride form, 100-200 mesh, BioRad Laboratories, Richmond, CA, U.S.A.) and gel filtration chromatography (Bio-Gel P-60, 100-200 mesh, BioRad Laboratories, Richmond, CA, U.S.A.). For the assay, a large pool of porcine serum was filtered through a hollow fiber filter system (Amicon Corp., Danvers, MA, U.S.A.) to remove pituitary hormones (exclusion limit $\geq 10,000$ molecular weight). Albumin from chicken eggs (Sigma Chemical Company, St. Louis, MO, U.S.A.) was added to the pool of filtered serum to give a 5% (w/v) solution (EA-FPS). Standard curves were prepared in EA-FPS to give between 0.05 and 10 ng USDA-pLH-I-1/200 µl EA-FPS. Binding of ^{125}I -pLH to antisera was similar for tubes containing 200 µl EA-FPS plus 300 µl assay buffer (0.1 M phosphate buffered saline with 1% bovine serum albumin, pH 7.5) and for tubes with 500 µl assay buffer. The antiserum (Chemicon International, Inc., El Segundo, CA, U.S.A.) did not crossreact significantly with USDA-pGH-B-1 (2.1%), USDA-pFSH-B-1 (0.2%), or USDA-pPRL-B-1 (<0.06%). Increasing volumes of sow serum displaced ^{125}I -pLH from the antisera to produce a binding curve that was parallel to the standard curve. When 0.3, 0.6, 1.2, 2.5, 5.0, and 10.0 ng USDA-pLH-I-1/ml were added to EA-FPS, 0.3, 0.4, 1.2, 2.4, 5.9, and 12.4 ng were recovered (average 99.2% recovery). Sensitivity of the assay was 0.17 ng/assay tube. All samples were

quantified in 5 assays and the intra- and inter-assay coefficients of variation were 9.4% and 11.6%, respectively.

FSH. Concentrations of FSH in porcine serum (pFSH) were determined by a double-antibody RIA similar to that described by Kraeling et al. (1982) for pLH. Purified pFSH (LER-1419-3, 2.5 μ g) was reacted with 10 μ g chloramine-T and 500 μ Ci 125 I. The reaction was stopped with 40 μ g sodium metabisulfite and 125 I-pFSH was separated from free 125 I as described above for 125 I-pLH. Albumin from bovine serum (Sigma Chemical Co., St. Louis, MO, U.S.A.) was added to filtered porcine serum to give a 5% (w/v) solution (BSA-FPS). Standard curves were prepared in BSA-FPS ranging from 0.128 to 32.0 ng LER-1419-3/200 μ l BSA-FPS. Binding of 125 I-pFSH to antisera was similar for tubes containing 200 μ l BSA-FPS plus 300 μ l assay buffer (0.1 M phosphate buffered saline with 1% bovine serum albumin, pH 7.5) and for tubes with 500 μ l assay buffer. The antiserum (Chemicon International, Inc., El Segundo, CA, U.S.A.) did not crossreact significantly (less than 0.1%) with USDA-pLH-I-1, USDA-pPRL-B-1, or USDA-pGH-B-1. Increasing volumes of sow serum displaced 125 I-pFSH from the antisera to produce a binding curve that was parallel to the standard curve. When 1, 2, 4, 8, 16, and 32 ng LER-1419-3/ml were added to BSA-FPS, 0.8, 1.6, 4.3, 9.6, 18.4, and 34.2 ng, respectively, were recovered (average 101.6% recovery). Sensitivity of the assay was 0.256 ng/assay tube. All samples were quantified in 5 assays and the intra- and inter-assay coefficients of variation averaged 3.8% and 12.1%, respectively.

Progesterone. Concentrations of progesterone in porcine serum were determined by RIA according to previously described procedures using a highly

specific progesterone antiserum (Stevenson et al., 1981). The antiserum was obtained by immunizing rabbits against progesterone-11-hemisuccinate:BSA (Q3253, Steraloids, Inc., Wilton, NH, U.S.A.). Standard progesterone (P0130, Sigma Chemical Co., St. Louis, MO, U.S.A.) in 95% ethanol only crossreacted (>1%) with 17 α -hydroxyprogesterone (13.8%), 5 α -pregnanedione (25.1%), 5 β -pregnanedione (8.1%), and 21-deoxycortisone (13.4%) of 19 steroids tested. Tritiated (1,2,6,7,16,17-³H) progesterone (TRK.621, Amersham, Chicago, IL, U.S.A.) was repurified by Sephadex LH20 (Pharmacia, Uppsala, Sweden) column chromatography using Iso-octane:Benzene (90:10, w/v) as column solvents. Extraction of ³H-progesterone from porcine serum averaged 81% in 10 assays. Progesterone was recovered quantitatively when added to serum (r=0.99) and increasing volumes of porcine serum displaced ³H-progesterone from a binding curve that paralleled the standard curve. Variable volumes (N=4) of porcine serum (25, 50, and 75 μ l) measured 24.7, 21.9, and 19.4 ng/ml, respectively. Sensitivity of the assay was 20 pg/tube. All samples were quantified in two assays and the intra- and inter-assay coefficients of variation averaged 9.7% and 10.7%, respectively.

Oestradiol. Concentrations of oestradiol-17 β in porcine serum were quantified in 4 RIAs according to previously described procedures (Kluber, Pollmann, Davis & Stevenson, 1985). Samples of serum (6 ml in duplicate) were extracted twice with ethyl acetate with extraction efficiency averaging 85% in 4 assays. The antiserum (oestradiol-6-3, N.R. Mason, Eli Lilly and Company, Indianapolis, IN, U.S.A.) utilized was highly specific for oestradiol-17 β . Crossreactivities with oestradiol-17 α , oestrone, oestriol, testosterone, and androstenedione were nil (<0.01%). Tritiated (2,4,6,7-³H) oestradiol-17 β

(TRK.322, Amersham, Chicago, IL, U.S.A.) was used as assay tracer and oestradiol-17 β (E-8875, Sigma Chemical Co., St. Louis, MO, U.S.A.) in 95% ethanol as the standard. Addition of 25, 50, or 100 pg oestradiol-17 β (N=4 each) to porcine serum yielded 28, 49, and 97 pg ($r=0.98$). Increasing volumes of porcine serum displaced ^3H -oestradiol-17 β from a binding curve that paralleled the standard curve. Sensitivity of the assay was 5 pg/tube. The intra- and inter-assay coefficients of variation averaged 8.3% and 11.1%, respectively.

Cortisol. Cortisol in serum was measured in 3 RIAs using a specific antiserum obtained from immunizing rabbits against cortisol-3-hemisuccinate:BSA (Western Chemical, Fort Collins, CO, U.S.A.). Specificity of antiserum was tested against 14 different steroids and only crossreacted slightly (at 50% binding inhibition of the labeled cortisol) with 11-deoxycortisol (7.5%), cortisone (0.6%), and progesterone (2.4%). Crossreactivity was nil with corticosterone (<0.1%), deoxycorticosterone (<0.1%), 21-deoxycortisone (<0.1%), 11 α -hydroxy-progesterone (<0.1%), 11 β -hydroxy-progesterone (<0.1%), 17 α -hydroxy-progesterone (<0.1%), 20 α -dihydro-progesterone (0.1%), 20 β -dihydro-progesterone (0.1%), pregnenolone (<0.1%), testosterone (<0.1%), and androstenedione (<0.1%). Tritiated (1,2,6,7- ^3H) cortisol (TRK.407, Amersham, Chicago, IL, U.S.A.) extracted from porcine serum with ethyl acetate was 88.5% in 3 assays. Standard cortisol (H-4001, Sigma Chemical Co., St. Louis, MO, U.S.A.) was recovered quantitatively when 50, 60, 80, 100, 120, 160, 200, 400, and 600 pg were added to 0.1 ml porcine serum, cortisol recovered was 58, 61, 75, 94, 124, 164, 223, 398, and 569 pg ($r=0.99$), respectively. Increasing volumes of porcine serum displaced ^3H -cortisol from

a binding curve that paralleled the standard curve. Variable volumes of serum (0.075, 0.1, 0.15, 0.2 ml, N=4 each) measured 9.9, 10.6, 9.5, and 8.5 ng/ml. Assay sensitivity was 20 pg/tube and intra- and inter-assay coefficients of variation were 10.9% and 11.3%, respectively.

Insulin. Concentrations of insulin in porcine serum were quantified in 4 assays using RIA kits for insulin (130K, Cambridge Medical Diagnostics, Inc., Billerica, MA, U.S.A.). Porcine insulin in assay buffer (borate buffer with EDTA and BSA) at concentrations of 5, 15, 35, 75, 150, and 300 μ U porcine insulin/ml was used for assay standards. A pool of porcine serum (control serum) was obtained from lactating sows and at least 4 control serum samples were included in each assay. The intra- and inter-assay coefficients of variation averaged 5.7% and 11.6%, respectively.

Thyroxine. Concentrations of thyroxine in porcine serum were quantified in 4 assays using RIA kits for tetraiodothyronine (156, Cambridge Medical Diagnostics, Inc., Billerica, MA, U.S.A.). Human thyroxine in assay buffer (barbital buffer with BSA) at concentrations of 1.0, 2.5, 5.0, 10.0, and 25.0 ng thyroxine/ml was used for assay standards. A pool of porcine serum (control serum) was obtained from lactating sows and at least 4 control serum samples were included in each assay. The intra- and inter-assay coefficients of variation were 5.2% and 5.8%, respectively.

Definitions

A rise in the concentration of LH was defined as a pulse using criteria previously established (Riley, Peters & Lamming, 1981; Mcleod, Haresign &

Lamming, 1982). An increase in serum LH was designated as a pulse when 1) the highest LH concentration attained was 50% above the preceding nadir; 2) at least 2 consecutive LH values were between the peak value and the following nadir value; and 3) the rate of decline from LH peak values was not greater than the half-life of LH, which is approximately 30 min in porcine serum (Esbenshade, Vogel & Traywick, 1986). Overall LH was defined as the average of all concentrations of LH within a sow-period, whereas baseline concentrations of LH were equivalent to the average of all LH concentrations within a sow-period after excluding peak values (all values within a pulse). Magnitude of LH pulses was defined as the highest value within a pulse, whereas amplitude of LH pulses was obtained by subtracting the baseline concentrations of LH from the magnitude of the LH pulse. Duration of LH pulses was defined as the interval from nadir to nadir.

Statistical analyses

Data were subjected to analysis of variance using the General Linear Model procedures of the Statistical Analysis System (SAS, 1982). Hormonal concentrations were analyzed as a split-plot analysis for repeated measurements. Analysis of variance included treatment (N=2), parity (primiparous vs multiparous), day, and treatment x day interactions. Treatment was tested by the between animal variance (animal within treatment). Pre-planned orthogonal contrasts were made to compare control multiparous (CM) sows with control primiparous (CP) and treated multiparous (TM) sows, and CP vs treated primiparous (TP) sows. Other traits (days to oestrus, feed intake of sows, and sow and litter weights at weaning) were analyzed with treatment and parity (N=2) plus two-way interactions as sources of variation.

Comparisons among treatment means were made by Scheffe's interval (Gill, 1978). Percentage comparisons were tested for independence by chi-square.

Results

Table 1 illustrates that lactation length, and litter size and weight were similar among treatment groups. As expected, multiparous sows weighed more ($P<0.05$) than primiparous sows. All of the TM sows (10/10) exhibited oestrus during lactation, whereas none of the TP (0/4), CM (0/2), or CP (0/2) sows returned to oestrus until after weaning (Table 2). Intervals to oestrus preweaning for CM sows were similar to postweaning intervals to oestrus for the other groups.

Preweaning Endocrine Patterns

Overall daily concentrations (average of 16 samples/day) of FSH and LH, and FSH to LH ratios are illustrated in Fig. 1 for all treatment groups. Overall FSH was already 1.5-fold higher ($P<0.05$) in primiparous than multiparous sows 1 day before LS + BE was initiated, and concentrations of FSH were higher ($P<0.05$) in TP (12.5 ng/ml) than TM (5.9 ng/ml) sows during days 0 to 3. In contrast to FSH, overall concentrations of LH were similar for primiparous and multiparous sows before treatment initiation (day -1), whereas concentrations of LH were higher ($P<0.05$) in TM (0.9 ng/ml) than CM (0.4 ng/ml) sows during LS + BE. Ratios of FSH to LH were 1.7-fold higher ($P<0.05$) in primiparous than multiparous sows before treatment (day -1), and FSH to LH ratios were greater ($P<0.05$) in TP (16.1) than TM (7.6) sows during days 0 to 3. Significant ($P<0.05$) treatment x day interactions were detected for overall concentrations of FSH and FSH to LH ratios. Patterns of LH and

FSH in serum on days -1, 0, 1, 2, and 3 from LS + BE are illustrated for one representative sow from each of the CM (Fig. 2), TM (Fig. 3), CP (Fig. 4), and TP (Fig. 5) groups whose secretory profile was close to the average of that treatment group.

Characteristics of pulsatile patterns of LH are summarized in Table 3 for each treatment group. Overall and baseline concentrations of LH were about 2-fold higher ($P<0.05$) in treated (TM and TP) than control (CM and CP) sows during days 0 to 3. Frequency of pulses of LH per 5 h were 1.5-fold higher ($P<0.05$) in TP than TM sows (2.0 vs 1.3/5 h), whereas duration, magnitude, and amplitude of LH pulses were similar across treatments.

Significant ($P<0.05$) treatment x day interactions were detected for number of LH pulses and baseline concentrations of LH. The interaction for baseline LH was caused by a doubling of baseline concentrations of LH from day -1 to days 0, 1, 2, and 3 for TM and TP sows, but not for control sows. A significant ($P<0.05$) day effect also was observed for the number of pulses of LH with a general decline in the frequency of pulses from day -1 to day 3. However, the treatment x day interaction was evident when comparisons were made among primiparous, but not multiparous sows. Frequency of pulses of LH per 5 h were similar between TM and CM sows, whereas the pattern of LH pulses decreased across days for CP sows; and first decreased and then increased for TP sows (Table 3). Although no significant differences were detected, duration of LH pulses increased 3 to 4-fold from day -1 to day 0 for both TM and TP sows.

Average daily concentrations of oestradiol-17 β (oestradiol), progesterone, cortisol, insulin, and thyroxine in serum are illustrated in Fig. 5 for all treatment groups.

Mean concentrations of oestradiol were already 2-fold greater ($P=0.08$) for multiparous than primiparous sows 1 day before LS + BE was initiated. Concentrations of oestradiol were higher ($P<0.01$) in TM (3.4 pg/ml) than CM (1.6 pg/ml) sows, and higher ($P<0.01$) in TM than TP (1.2 pg/ml) sows during days 0 to 3. Concentrations of oestradiol increased 2.2-fold from day 0 to day 3 for TM sows (Fig. 5).

Average daily concentrations of progesterone in serum were similar for all treatment groups before LS + BE (day -1). However, average progesterone was higher ($P<0.05$) for TP (0.6 ng/ml) than CP (0.3 ng/ml) sows during days 0, 1, and 2. Progesterone in serum increased 3-fold from day 0 to day 1, and then decreased to initial (day -1) concentrations by day 3 for TP sows. In TM sows, progesterone increased 2.6-fold from day 0 to day 1, and then declined to levels similar to day 0 concentrations by day 3 (Fig. 5).

Mean concentrations of cortisol in serum were already higher ($P<0.05$) for multiparous (9.1 ng/ml) than primiparous (6.9 ng/ml) sows before treatment initiation (day -1). Levels of cortisol were higher ($P<0.01$) for TM (16.0 ng/ml) than CM (10.9 ng/ml) sows on days 0, 1, 2, and 3, whereas concentrations of cortisol were higher ($P<0.01$) for TP (14.8 ng/ml) than CP (11.0 ng/ml) sows on days 0, 1, and 2. A significant ($P<0.05$) treatment \times day interaction was detected for cortisol and was caused by a 2 to 3.5-fold increase in concentrations of cortisol from day -1 to day 0 for treated (TM and TP) sows, but not for control sows. A significant ($P<0.05$) day effect also was observed

with a sharp rise in cortisol from day -1 to day 0 in response to LS + BE and a slight decline from day 0 to day 3 (Fig. 5).

Average daily concentrations of insulin in serum were similar for primiparous and multiparous sows before LS + BE (day -1). Concentrations of insulin were almost 2-fold higher ($P < 0.005$) in CM (48.8 $\mu\text{U/ml}$) than TM (25.3 $\mu\text{U/ml}$) sows on days -1, 0, 1, and 2, whereas concentrations of insulin were similar for CP and TP sows. A significant ($P < 0.05$) day effect was observed with concentrations of insulin decreasing by one-third from day -1 to day 0, increasing to initial (day -1) levels from day 0 to day 1, and decreasing again to day 0 concentrations from day 1 to day 2 (Fig. 5).

Mean daily concentrations of thyroxine in serum were similar for all treatment groups before initiation of LS + BE (day -1), as well as on days 0, 1, and 2 during treatment. A significant ($P < 0.05$) treatment \times day interaction was detected for concentrations of thyroxine and was caused by an attenuation of day -1 levels to day 0 in TP sows. In all other groups, concentrations of thyroxine decreased by one-third to one-half from day -1 to day 0. A significant ($P < 0.05$) day effect also was observed with levels of thyroxine decreasing from day -1 to day 0, and thereafter maintained at day 0 concentrations (Fig. 5).

Postweaning Endocrine Patterns

Overall daily concentrations (average of 16 samples per day) of FSH and LH, and FSH to LH ratios are illustrated in Fig. 6 for CM, CP, and TP sows. Although not significant, concentrations of FSH were 1.5-fold higher for CP and TP (10.1 ng/ml) sows than for CM (6.9 ng/ml) sows 1 day before weaning (day -1), whereas concentrations of FSH were similar on days 0, 1, and 2.

Although not significant, overall concentrations of LH were 2-fold greater for TP (0.8 ng/ml) than CM and CP (0.4 ng/ml) sows before weaning (day -1) with concentrations of LH remaining similar on days 0, 1, and 2 for all treatment groups. Ratios of FSH to LH were similar for all groups on days -1, 0, 1, and 2.

Significant ($P < 0.05$) treatment \times day interactions were noted for overall concentrations of FSH and FSH to LH ratios. The interaction for overall FSH seemed to be caused by a decrease in concentrations of FSH from day 0 to day 3 for CM sows, but not for CP or TP sows (Fig. 6). Significant ($P < 0.05$) day effects were observed for overall concentrations of FSH and LH, and FSH to LH ratios. A day effect across treatments for overall FSH was caused apparently by a decrease in FSH from day 0 to day 1, and an increase in FSH from day 1 to day 3. Day effects for overall LH, and FSH to LH ratios were caused by increased concentrations of gonadotropins from day -1 to day 0. Patterns of LH and FSH in serum on days -1, 0, 1, and 2 from weaning are illustrated for a representative sow whose secretory profile was close to the average of each treatment group are illustrated in Fig. 7 (CM), Fig. 8 (CP), and Fig. 9 (TP).

Characteristics of pulsatile patterns of LH are summarized in Table 4 for CM, CP and TP sows. Number of pulses of LH per 5 h was 1.7-fold higher ($P < 0.05$) in TP than CM and CP (3.2 vs 1.9/5 h) sows on days 0, 1, and 2 from weaning. Baseline concentrations of LH, and duration, magnitude, and amplitude of pulses of LH were similar among treatment groups.

A significant ($P < 0.05$) day effect was observed for baseline concentrations and number of pulses of LH (Table 4). Average baseline concentrations of LH in serum increased 4 to 5-fold for control sows from day

-1 to day 0. Within hours of weaning, baseline concentrations of LH had increased in control sows, whereas TP sows had no shift in the baseline LH. However, number of pulses of LH nearly doubled in TP sows from 2.7 to 4.3 pulses per 5 h from day -1 to day 0, whereas change in pulse frequency for control sows on those days was not consistent.

Mean daily concentrations of oestradiol, progesterone, cortisol, insulin, and thyroxine in serum are illustrated in Fig. 10 for CM, CP and TP groups.

Average concentrations of oestradiol were similar for all treatment groups 1 day before weaning (day -1), whereas concentrations of oestradiol were 1.5-fold higher ($P<0.05$) for CP (4.6 pg/ml) than TP (3.1 pg/ml) sows on days 1 and 2 postweaning. A significant ($P<0.05$) treatment x day interaction was detected for concentrations of oestradiol on days 0, 1, and 2 from weaning. A significant ($P<0.05$) day effect also was observed for oestradiol and appeared to be due to a linear increase in concentrations of oestradiol from day -1 to day 2 from weaning, especially in control (CM and CP) sows (Fig. 10).

Concentrations of progesterone in serum were similar for all treatment groups on days -1, 0, 1, and 2 from weaning. No treatment x day interaction nor day effects were detected for average daily concentrations of progesterone for all treatment groups after weaning (Fig. 10).

Concentrations of cortisol in serum were similar across treatment groups despite a numerical difference of 1.3-fold higher cortisol in serum of CP and TP sows compared to CM sows 1 day before weaning (day -1). Cortisol levels also were similar on days 0, 1, and 2 from weaning for all treatment groups. A significant ($P<0.05$) day effect was noted for concentrations of cortisol in

serum and was caused by a doubling of cortisol levels from day -1 to day 0, and a subsequent decline of serum cortisol from day 0 to day 2 (Fig. 10).

Concentrations of insulin in serum were similar for all treatment groups 1 day before weaning despite 2-fold higher concentrations of insulin in serum of TP (21.2 μ U/ml) than CP (13.7 μ U/ml) sows. Although not significant, levels of insulin were higher in CM (21.1 μ U/ml) than CP or TP (18.8 μ U/ml) sows on days 0, 1, and 2 from weaning. A significant ($P < 0.05$) day effect for concentrations of insulin was observed, and was probably due to a 60% decrease in the concentrations of insulin from day -1 to day 0, and a subsequent 3-fold increase in insulin within 24 h after weaning.

Concentrations of thyroxine in serum were similar for all treatments on days -1, 0, 1, and 2 from weaning, despite a 1.5-fold difference in levels of thyroxine for CM (28.3 ng/ml) compared with CP and TP (18.5 ng/ml) sows. A significant ($P < 0.05$) day effect was observed for concentrations of thyroxine, and was due to a 2-fold increase in thyroxine from day 0 to day 1 from weaning.

Discussion

This study has provided new information about endocrine factors involved in stimulating oestrous cyclicity and subsequent reproductive function during and after lactation in sows. Our experiment was designed to address several concepts concerning the 1) influences of LS + BE on concentrations of hormones in serum responsible for inducing oestrus during lactation; 2) differences in hormonal patterns between primiparous and multiparous sows in response to LS + BE and weaning that may explain why primiparous sows have delayed intervals to oestrus; and 3) similarity between hormonal secretory patterns for sows that express oestrus during lactation or after weaning.

Before treatment (LS + BE) was initiated during lactation, some differences in hormonal concentrations between primiparous and multiparous sows were evident. Concentrations of FSH in serum were higher in primiparous than multiparous sows, whereas levels of cortisol and oestradiol were greater in multiparous than primiparous sows before treatment. Differences in hormonal concentrations may reflect partly differences in ovarian follicular growth. Palmer et al. (1965) and Kunavongkrit et al. (1982) reported that multiparous sows have more ovarian follicles than primiparous sows during lactation, and follicular size was greater in multiparous than primiparous sows (≥ 5 mm vs 2-4.99 mm, respectively). If multiparous sows have more, as well as larger follicles, we would expect 1) secretion of oestradiol to be greater in multiparous sows; and 2) negative feedback of some ovarian factor (possibly inhibin) on secretion of FSH to be greater in multiparous than primiparous sows (Stevenson et al., 1981). Both expectations were observed as oestradiol was greater and FSH was lower in multiparous sows.

Litter separation and BE immediately increased baseline concentrations and pulse frequency of LH in treated compared with control sows. These data confirm earlier reports in which altered suckling patterns of piglets (i.e., weaning) increased LH secretion (Duggan et al., 1982; Stevenson & Britt, 1980; Aherne, Christopherson, Thompson & Hardin, 1976; Edwards & Foxcroft, 1983; Kirkwood, Lapwood, Smith & Anderson, 1984; Shaw & Foxcroft, 1985). We also noted that frequency of pulses of LH were higher in TP than TM sows, perhaps reflecting age or parity differences in sensitivity to gonadotropin secretion or greater inhibition of LH by increased titers of oestradiol in TM sows.

Litter separation + BE during lactation also affected concentrations of cortisol and progesterone in serum. Treatment resulted in an immediate increase in cortisol (TM and TP), and a somewhat delayed increase in progesterone concentrations (TP) compared with control sows. Increased concentrations of cortisol in serum of treated sows probably reflects sow response to physical movement, unfamiliar pens, and encounters with boars (Barnett, Hemsworth & Cronin, 1982). Cortisol may have an adverse effect on secretion of LH during lactation and after weaning (Liptrap, 1970; Schilling & Von Rechenberg, 1973; Barb, Kraeling, Rampacek, Fonda & Kiser, 1982; Kunavongkrit et al., 1984). Increased progesterone in serum of treated sows on day 1 after LS + BE may reflect an ovarian response to increased secretion of LH. Increased secretion of cortisol and progesterone may have inhibited further follicular growth and(or) ovulation in TP but not TM sows.

Our study points to an apparent lack of follicular growth and increased secretion of cortisol and progesterone to be among the main factors inhibiting oestrous cyclicity during lactation in TP sows. Richards (1980) suggested that changes in ovarian follicular function in suckled beef cows (i.e., from

synthesis of progesterone to oestradiol) may be associated with changes in number of follicular gonadotropin binding sites. However, Spicer, Convey, Leung, Short & Tucker (1986) reported that changes in numbers of ovarian LH and FSH receptors were not associated with increased oestradiol production in large follicles during the post partum anovulatory period in suckled beef cows. They suggested that initial intra-ovarian events that lead to selection of ovulatory follicles first involve increased production of progesterone and capacity to bind LH, and then an increased capacity to produce oestradiol and bind FSH in large follicles. Increased capacity of follicles to bind LH also has been observed during preovulatory follicular development in pigs (Stouffer, Tyrey & Schomberg, 1976), sheep (Webb & England, 1982a;b), and rats (Uilenbroek & Richards, 1979).

Only multiparous (TM) sows exhibited oestrus during lactation; therefore, it was not impossible to separate completely the effects of treatment and parity in our experiment, as the two factors were confounded. In our previous studies, about 45% of the primiparous sows and 76% of the multiparous sows were in oestrus during lactation after LS + BE. All of our previous studies were conducted during winter (October to December), whereas this study was in May and we observed no oestrous response for primiparous sows in May and no response for both parities in August (Newton, Stevenson & Davis, 1986). Furthermore, understanding why fewer primiparous than multiparous sows are estrual after LS + BE is not clear. However, differences in hormonal patterns between primiparous and multiparous sows in response to LS + BE were due mainly to differences in secretion of oestradiol and FSH; the former being greater in TM sows, whereas the latter was higher in TP sows. Moreover, concentrations of oestradiol and FSH probably reflect differences in ovarian

follicular growth between parities with multiparous sows having more and larger ovarian follicles than primiparous sows. Differences in follicular growth at weaning also may account for the differences in intervals to postweaning oestrus between primiparous and multiparous sows that are reported commonly (Rasbech, 1969; Aumaitre, Dagorn, Legault & LeDenmat, 1976; King, 1978; Fahmy, Holtmann & Baker, 1979; Hurtgen, Leman & Crabo, 1980; Karlberg, 1980; Benjaminsen & Karlberg, 1981; Szarek, Levis & Britt, 1981; Hemsworth, Salden & Hoogerbrugge, 1982). Perhaps primiparous sows require more time for ovarian follicular growth than multiparous sows, resulting in increased intervals to oestrus.

One observation concerning the differences in gonadotropin secretion for TP and CP sows just prior to weaning is somewhat baffling. Even though TP sows failed to come into oestrus during lactation, frequency of their LH pulses were already greater and concentrations of LH and FSH tended to be greater than those of CP sows before weaning. Despite these differences, intervals to oestrus for all primiparous sows were similar. Furthermore, patterns of endocrine secretion for CP sows at weaning were markedly similar to those of TP sows during lactation. These results suggest that some other factors may be inhibiting the onset of oestrus besides the re-establishment of increased pulse frequency of LH and changes in FSH in serum. Further work addressing these hormonal factors that initiate oestrus are needed to elucidate the role of changing concentrations and pulse frequencies of the gonadotropins.

It is interesting to note the marked similarities of hormonal secretory patterns for sows that expressed oestrus during lactation (TM) or after weaning (CM, CP, and TP sows). Concentrations of FSH in serum and FSH to LH ratios were relatively high 1 day before LS + BE (TM) and weaning (CM, CP, TP) and

then decreased progressively over time (Fig. 1 and Fig. 6). Pulsatile patterns of secretion of LH also appeared similar for sows in oestrus during lactation and after weaning, as did increases in baseline concentrations of LH. Cortisol in serum increased on the day of LS + BE and weaning, and gradually decreased thereafter. Oestradiol increased progressively from day 0 to day 3 from LS + BE and weaning. The only reproductive hormone in which secretory patterns were different during lactation and after weaning was progesterone. Concentrations of progesterone in serum did not increase 24 h after weaning in CM, CP, or TP sows, whereas levels of progesterone increased 24 h after the onset of LS + BE for both TM and TP sows. Cox & Britt (1982) reported that progesterone was elevated in gonadotropin-releasing hormone (GnRH)-treated sows before and during oestrus, but this elevation did not interfere with oestrus or conception. However, Knobil (1980) reported that elevated levels of progesterone during pulsatile GnRH infusion in hypothalamic-lesioned monkeys may have contributed to their failure to initiate menstrual cycles. For the most part, it appears that sows that resume oestrous cyclicity during lactation are responding both endocrinologically and physiologically as weaned sows. Previous research supports this observation (Rowlinson & Bryant, 1976; Stevenson & Davis, 1984). It is also interesting to note that in this experiment and a previous one (Stevenson & Davis, 1984), sows that exhibited oestrus during lactation generally required about 1 day longer to express oestrus when compared with sows in oestrus after weaning. A physiological reason for this delay may be the increase in concentrations of progesterone reported in sows that are LS + BE during lactation.

Coupled with the results from a companion paper (Newton, Stevenson & Davis, 1986), the present study suggests that 1) altering suckling patterns of

piglets can induce oestrus cyclicity in lactating sows; 2) sows that respond to LS + BE have hormonal secretory patterns similar to sows that return to oestrus after weaning; 3) multiparous sows probably have more and larger ovarian follicles (Kunavongkrit et al., 1982) and increased oestradiol secretion than primiparous sows resulting in more multiparous sows in oestrus during lactation; and 4) increased secretion of progesterone and possibly cortisol may inhibit oestrous cyclicity in primiparous, but not multiparous sows.

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Table 1. Sow and litter performance after litter separation and boar exposure during lactation and at weaning

Treatment group ^a	No. sows	Days post partum	Litter size piglets/sow	Sow weight at weaning, kg	Litter weight at weaning, kg
CM	2	19.0	7.5 ± 0.7	183.3 ± 13.5 ^b	52.7 ± 5.9
TM	10	19.6 ± 1.3	8.0 ± 1.1	187.9 ± 6.3 ^b	56.5 ± 2.7
CP	2	18.5 ± 4.9	8.5 ± 2.1	160.8 ± 13.6 ^c	55.9 ± 5.9
TP	4	17.5 ± 1.9	7.0	166.0 ± 10.3 ^c	49.3 ± 4.5

^aCM = Control multiparous, TM = Treated multiparous, CP = Control primiparous, and TP = Treated primiparous.

^{b,c}Means with different superscripts differ ($P < 0.05$).

Table 2. Occurrence of oestrus in sows after litter separation and boar exposure during lactation and after weaning

Treatment group ^a	No. sows	No. sows exhibiting LE ^b	Oestrous characteristics		
			Days to oestrus from treatment	Days to oestrus from weaning	
CM	2	0	10.9 \pm 0.5 ^d	3.0 \pm 0.5	
TM	10	10	5.2 \pm 0.5 ^c		
CP	2	0	12.0 \pm 0.5 ^d	4.0 \pm 0.5	
TP	4	0	13.0 \pm 0.3 ^d	5.0 \pm 0.3	

^aCM = Control multiparous, TM = Treated multiparous, CP = Control primiparous, and TP = Treated primiparous.

^bLE = Lactational oestrus.

^{c,d}Means with different superscripts differ ($P < 0.05$).

Fig. 1. Concentrations of FSH and LH, and FSH to LH ratios in treated primiparous (TP), treated multiparous (TM), control primiparous (CP), and control multiparous (CM) sows from litter separation and boar exposure (LS + BE).

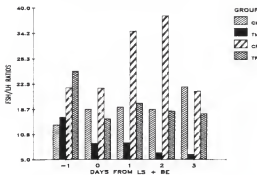
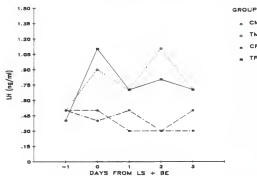
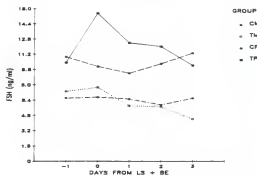


Fig. 2. Pulsatile secretion of LH and FSH in B29 (control multiparous; CM) from litter separation and boar exposure (LS + BE). Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from LS + BE.

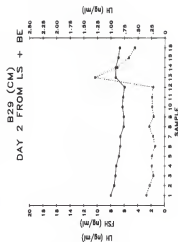
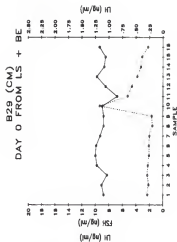
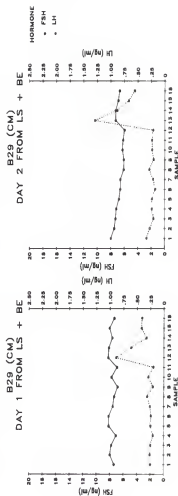
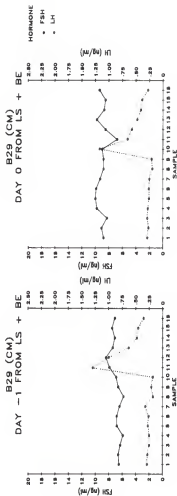


Fig. 3. Pulsatile secretion of LH and FSH in B25 (treated multiparous; TM) from litter separation and boar exposure (LS + BE). Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from LS + BE.

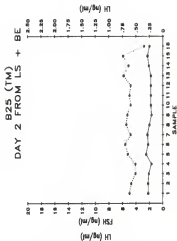
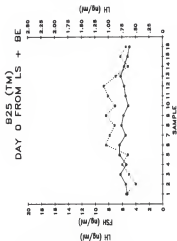
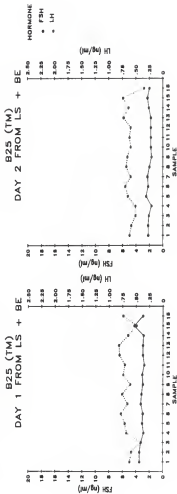
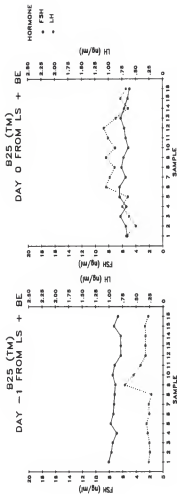


Fig. 4. Pulsatile secretion of LH and FSH in B36 (control primiparous; CP) from litter separation and boar exposure (LS + BE). Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from LS + BE.

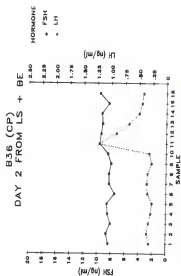
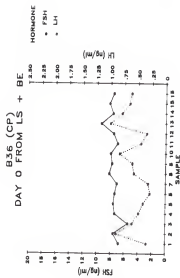
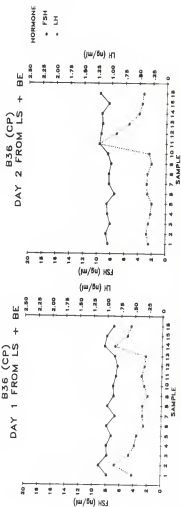
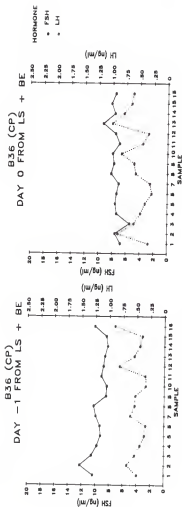


Fig. 5. Pulsatile secretion of LH and FSH in B53 (treated primiparous; TP) from litter separation and boar exposure (LS + BE). Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from LS + BE.

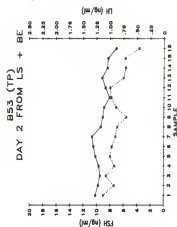
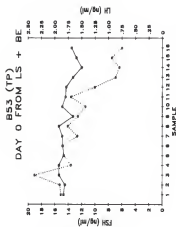
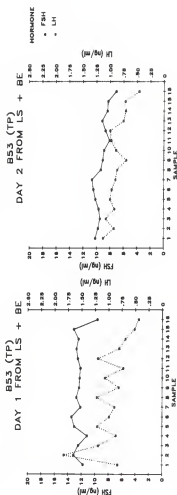
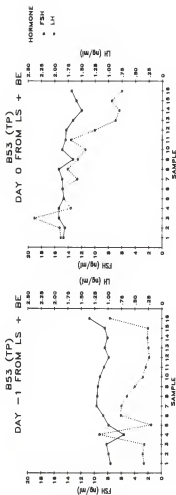


Table 3. Overall mean FSH and LH, and baseline concentrations of LH in control and altered suckled sows

Item	Days from litter separation and boar exposure					Treatment means \pm SE
	-1	0	1	2	3	
Overall FSH ^a , ng/ml						
CM	6.6	6.7	6.5	5.9	6.6	6.4 \pm 1.9 ^d
TM	7.3	7.7	5.8	5.7	4.4	6.2 \pm 1.0
CP	10.9	9.9	9.2	10.2	11.3	10.3 \pm 1.9
TP	10.3	15.5	12.4	12.0	10.0	12.0 \pm 1.3
Day means	8.3 ^b	9.5 ^c	7.7 ^d	7.6 ^d	6.7 ^e	
Overall LH ₁ ng/ml						
CM	.5	.4	.5	.3	.3	.4 \pm .03 ^g
TM	.5	.9	.7	1.1	.7	.8 \pm .01
CP	.5	.5	.3	.3	.5	.4 \pm .03
TP	.4	1.1	.7	.8	.7	.7 \pm .03
Day means	.5	.9	.6	.9	.6	
Avg. baseline LH ^a , ng/ml						
CM	.4	.3	.4	.3	.3	.3 \pm .03 ^h
TM	.4	.7	.6	.7	.7	.6 \pm .01
CP	.3	.3	.3	.3	.3	.3 \pm .03
TP	.3	.6	.5	.6	.5	.5 \pm .02
Day means	.4	.6	.5	.6	.5	

^aTreatment x day interaction (P<0.05).^{b,c,d,e}Means with different superscripts differ (P<0.05).^fOrthogonal contrast: TM vs TP (P<0.05).^gOrthogonal contrast: CM vs TM (P<0.05).^hOrthogonal contrast: CM vs TM and CP vs TP (P<0.05).

Table 4. Characteristics of pulsatile secretion of LH in control and altered suckled sows

Item	Days from litter separation and boar exposure					Treatment means \pm SE
	-1	0	1	2	3	
No. LH pulses ^a /5 h						
CM	1.5	1.0	1.5	1.0	.5	1.1 \pm .1 ^e
TM	1.9	1.1	1.7	1.0	.6	1.3 \pm .1
CP	2.5	2.0	1.0	.5	1.5	1.5 \pm .1
TP	2.0	1.0	2.5	2.0	2.5	2.0 \pm .1
Day means	1.9 ^c	1.2 ^{cd}	1.8 ^{cd}	1.2 ^{cd}	1.1 ^d	
Duration of LH pulses, min						
CM	100	100	65	120	86	94 \pm 4.2
TM	67	192	99	114	92	112 \pm 1.9
CP	103	110	97	137	115	113 \pm 4.2
TP	65	230	79	87	82	109 \pm 3.0
Day means	74 ^d	181 ^c	88 ^d	112 ^{cd}	97 ^d	
Magnitude of LH pulses, ng/ml						
CM	1.2 (.3) ^b	.9 (.5)	.9 (.5)	.8 (.5)	.7 (.3)	.9 \pm .03
TM	.9 (.5)	1.2 (.6)	.9 (.3)	1.7 (.3)	.9 (.5)	1.1 \pm .02
CP	1.2 (.9)	1.1 (.8)	1.1 (.8)	1.5 (1.2)	1.5 (1.2)	1.3 \pm .03
TP	.7 (.4)	1.6 (1.0)	1.1 (.6)	1.1 (.6)	1.2 (.8)	1.2 \pm .03
Day means	.9 (.6)	1.3 (.7)	.9 (.5)	1.3 (.5)	1.2 (.7)	

^aTreatment \times day interaction ($P < 0.05$).^bValues in parentheses are means for LH pulse amplitude, ng/ml.^{c,d}Means with different superscripts differ ($P < 0.05$).^eOrthogonal contrast: TM vs TP ($P < 0.05$).

Fig. 6. Concentrations of oestradiol, progesterone, and cortisol in treated primiparous (TP), treated multiparous (TM), control primiparous (CP), and control multiparous (CM) sows from litter separation and boar exposure (LS + BE).

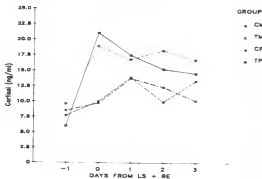
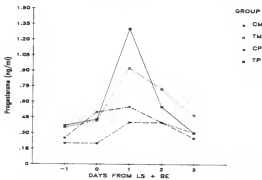
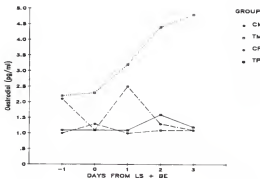


Fig. 7. Concentrations of insulin and thyroxine in treated primiparous (TP), treated multiparous (TM), control primiparous (CP), and control multiparous (CM) sows from litter separation and boar exposure (LS + BE).

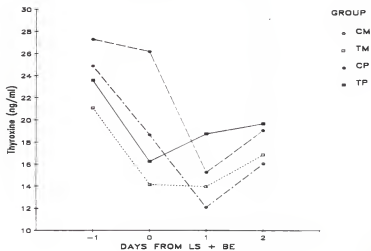
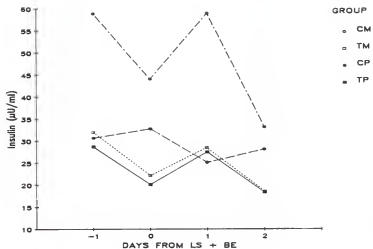


Fig. 8. Concentrations of FSH and LH, and FSH to LH ratios in treated primiparous (TP), control primiparous (CP), and control multiparous (CM) sows from weaning.

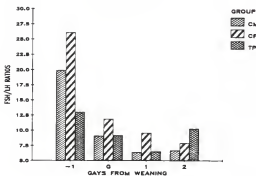
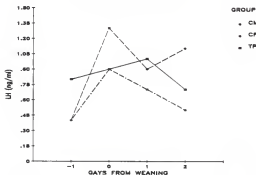
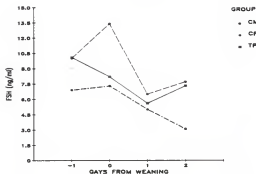


Fig. 9. Pulsatile secretion of LH and FSH in B29 (control multiparous; CM) from weaning. Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from weaning.

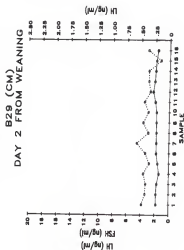
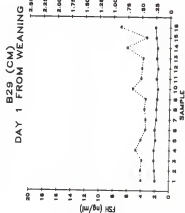
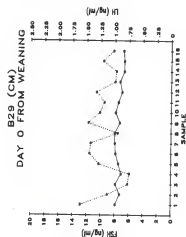
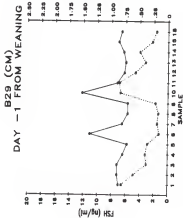


Fig. 10. Pulsatile secretion of LH and FSH in B36 (control primiparous; CP) from weaning. Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from weaning.

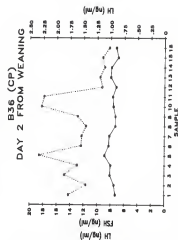
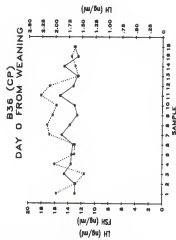
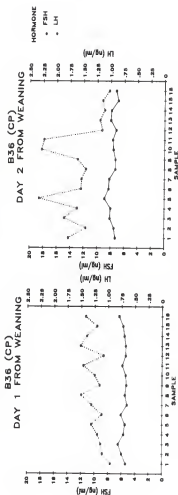
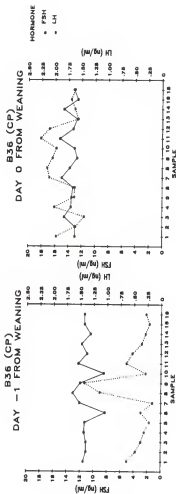


Fig. 11. Pulsatile secretion of LH and FSH in B53 (treated primiparous; TP) from weaning. Concentrations of gonadotropins were measured in serum collected at 20-min intervals for 5 h on each of 4 days (-1, 0, 1, and 2) from weaning.

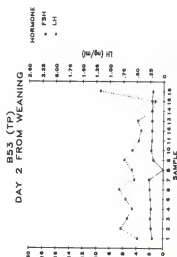
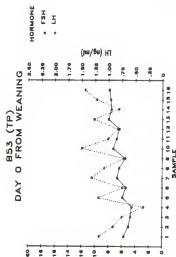
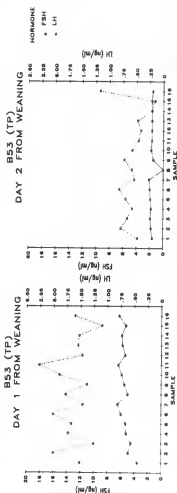
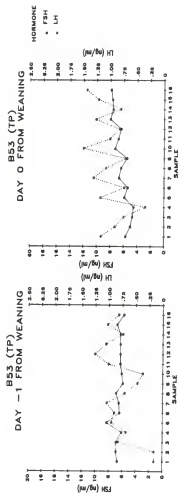


Table 5. Overall mean FSH and LH, and baseline concentrations of LH in control and altered suckled sows

Item	Days from weaning				Treatment means \pm SE
	-1	0	1	2	
Overall FSH ^a , ng/ml					
CM	6.9	7.3	5.0	3.1	5.6 \pm 1.9
CP	10.0	13.4	6.5	7.7	9.4 \pm 1.9
TP	10.1	8.2	5.6	7.3	7.8 \pm 1.3
Day means	9.3 ^b	9.3 ^b	5.7 ^c	6.4 ^d	
Overall LH, ng/ml					
CM	.4	.9	.7	.5	.6 \pm .05
CP	.4	1.3	.9	1.1	.9 \pm .05
TP	.8	.9	1.0 ^{bc}	.7 ^{bc}	.8 \pm .03
Day means	.6	1.0 ^c	.9	.7	
Avg. baseline LH, ng/ml					
CM	.2	.8	.6	.5	.5 \pm .05
CP	.2	1.1	.8	1.1	.8 \pm .05
TP	.5	.5	.8	.6 ^{bc}	.6 \pm .03
Day means	.3	.7	.8	.7	

^aTreatment \times day interaction ($P < 0.05$).

^{b,c,d}Means with different superscripts differ ($P < 0.05$).

Table 6. Characteristics of pulsatile secretion of LH in control and altered suckled sows

Item	Days from weaning				Treatment means \pm SE
	-1	0	1	2	
No. LH pulses/5 h					
CM	2.5	1.5	2.5	0	1.6 \pm .1 ^d
CP	2.0	2.5	3.0	1.0	2.1 \pm .1
TP	2.7 ^{bc}	4.3 ^b	3.3 ^b	2.5	3.2 \pm .1
Day means	2.5 ^{bc}	3.1 ^b	3.0 ^b	1.5 ^c	
Duration of LH pulses, min					
CM	80	79	55	58	71 \pm 1.5
CP	70	86	56	67	67 \pm 1.5
TP	88	70	69	66	73 \pm 1.5
Day means	81	77	62		
Magnitude of LH pulses, ng/ml					
CM	.7 (.5) ^a	1.5 (.5)	1.0 (.4)	2.0 (.9)	1.1 \pm .04
CP	.9 (.7)	1.6 (.5)	1.1 (.3)	1.1 (.5)	1.4 \pm .04
TP	1.2 (.8)	1.3 (.7)	1.3 (.5)	1.3 (.6)	1.2 \pm .03
Day means	1.0 (.7)	1.4 (.6)	1.2 (.4)		

^a Values in parentheses are means for LH pulse amplitude, ng/ml.^{b,c} Means with different superscripts differ ($P < 0.05$).^d Orthogonal contrast: CM + CP vs TP ($P < 0.05$).

Fig. 12. Concentrations of oestradiol, progesterone, and cortisol in treated primiparous (TP), control primiparous (CP), and control multiparous (CM) sows from weaning.

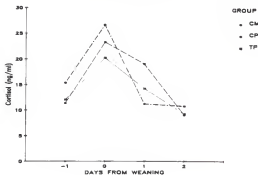
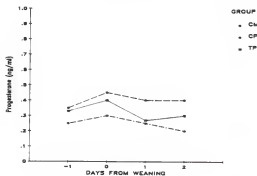
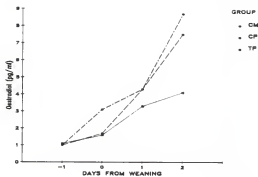
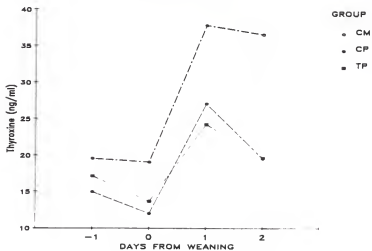
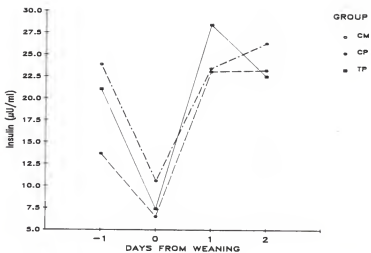


Fig. 13. Concentrations of insulin and thyroxine in treated primiparous (TP), control primiparous (CP), and control multiparous (CM) sows from weaning.



INFLUENCE OF ALTERED SUCKLING AND BOAR EXPOSURE ON SOWS:
ESTROUS RESPONSE AND ENDOCRINE CHANGES ASSOCIATED WITH
LACTATIONAL AND POSTWEANING ESTRUS

by

ELIZABETH ARRINGTON NEWTON

B.S., North Carolina State University, 1981

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Animal Sciences and Industry

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1986

ABSTRACT

Experiments were conducted to characterize estrous and endocrine relationships associated with altered suckling and boar exposure (BE) during lactation and after weaning in sows. To determine the influence of duration of litter separation (LS) with BE (1 h/d) on lactational estrus, 13 primiparous and 26 multiparous sows were separated from their litters for 3 or 6 h/d beginning 8 d before weaning in October and December, 1983. Percentage of sows in estrus during lactation was similar for 3 (65%) or 6-h (79%) periods of LS. Preweaning intervals to estrus for sows who expressed lactational estrus tended to be less for 6 (4.8 d) than 3-h (5.7 d) sows. More multiparous (88%) than primiparous (38%) sows were in estrus before weaning. Days to estrus for sows in estrus before and after weaning were less in multiparous than primiparous sows. These results indicated that duration of LS was not critical for inducing estrus as long as BE was provided. An experiment with 27 sows of mixed parity was conducted to partition the effects of LS (3 vs 6 h) and BE (0 vs 1 h) on lactational estrus in a 2 x 2 factorial experiment in August, 1985. No sows were in estrus during lactation, and neither LS nor BE altered intervals to postweaning estrus. Two more trials were conducted (October and November, 1985) with 46 primiparous sows in a design similar to that described previously. More LS (8/26) than non-LS (0/20) sows were in estrus preweaning; five were BE and three were non-BE. Non-BE sows also tended to have shorter preweaning intervals to estrus. LS and/or BE had no effect on intervals to postweaning estrus. These results indicated that season may inhibit induction of estrous cyclicity in sows exposed to boars and separated from their litters during lactation. Intervals to estrus before and

after weaning were similar for sows in all treatments regardless of when estrus was manifested.

To determine endocrine changes associated with LS (6 h/d) and BE (1 h/d) during lactation and after weaning, an experiment was conducted with 12 multiparous and six primiparous sows in May, 1985. Blood was collected every 15 min for 5 h on d -1, 0, 1, 2, and 3 from LS + BE (d 0) for all sows and on d -1, 0, 1, and 2 from weaning (d 0) for those sows who failed to express estrus during lactation. All (10/10) multiparous sows receiving LS + BE returned to estrus during lactation. None of the treated primiparous (0/4) nor control (0/4) sows returned to estrus until after weaning. Baseline concentrations of LH and FSH in serum were higher in LS + BE sows than controls. Number of pulses of LH was 1.5-fold greater for primiparous than multiparous sows during lactation. Insulin was higher in control multiparous (CM) sows than multiparous LS + BE sows (TM), whereas thyroxine in serum was unaffected. Estradiol-17 β increased in serum during LS + BE treatment and was higher in TM than CM or control primiparous (CP) sows. Prewaning cortisol and progesterone in daily serum pools were higher in TM than CM sows.

Number of pulses of LH was greater in treated primiparous (TP) than in control (CM or CP) sows after weaning. Estradiol in serum was higher in control (CM and CP) sows than TP sows after weaning. Insulin and thyroxine in serum were similar for sows in all groups after weaning. Results from this experiment indicated that LS and BE stimulated secretion of gonadotropins in treated sows. However, an apparent lack of ovarian follicular development coupled with low estradiol secretion in primiparous sows precluded estrous cyclicity during lactation, despite increased secretion of FSH and LH in serum compared with multiparous sows.

Overall, these experiments demonstrated that 1) disruption of suckling patterns of piglets is more essential than boar exposure to induce successfully estrous cyclicity in lactating sows; 2) multiparous sows are more responsive to treatments imposed during lactation than primiparous sows relative to estrous expression; 3) LS and BE increased number of pulses of LH and baseline secretion of FSH and LH during lactation; and 4) lack of apparent follicular development and estradiol secretion may explain partially why primiparous sows are less responsive to lactational treatments than multiparous sows.