Control of follicular development during and after lactation in sows

J. H. Britt, J. D. Armstrong, Nancy M. Cox* and K. L. Esbenshade

Department of Animal Science, Box 7621, North Carolina State University, Raleigh, NC 27695-7621 U.S.A.

Summary. Follicular development during early lactation in the sow is characterized by a large population of small-sized follicles and a small population of medium-sized follicles. As lactation progresses there is a gradual shift in number of follicles into medium- or large-sized categories and the percentage of follicles classified as atretic declines. Weaning at birth often leads to aberrant follicular development, apparently because the positive feedback response of LH to oestradiol does not occur during the first week *post partum*. Secretion of LH during lactation is primarily controlled by suckling intensity of the litter while FSH is controlled by a nonsteroidal ovarian factor, presumably inhibin. Suckling apparently limits secretion of GnRH and weaning leads to an increase of GnRH within the hypothalamus coincident with an increase of LH in the anterior pituitary and plasma and increased follicular growth. Follicular development during both lactation and post-weaning anoestrus can be stimulated by exogenous gonadotrophins and pulsatile administration of GnRH. Factors such as nutrition, season, boar exposure, litter size and split weaning affect follicular development during lactation and after weaning, probably because they affect secretion of LH.

Introduction

The domestic sow generally remains anoestrous during the first 4–6 weeks of lactation. Weaning the litter typically leads to a rapid increase in the size of antral follicles that culminates in oestrus and ovulation within 3 to 10 days. During lactation, therefore, the population of antral follicles is maintained in a state of readiness and is capable of responding to changes in secretion of gonadotrophins after weaning.

Follicular development during lactation and after weaning is influenced by several factors. For example, parity, season of year, nutrition, suckling intensity of the litter, exposure to mature boars and treatment with various hormones affect follicular development. The purpose of this paper is to review what is known about follicular development during and after lactation in sows and to describe how factors which affect follicular development exert their effects through the sow's endocrine system.

Follicular growth during and after lactation

Little is known about the distribution of follicles of different sizes during lactation. Before weaning most follicles are < 5 mm in diameter; however, weaning results in an immediate growth of follicles to more than 8 mm in diameter (Warnick, Casida & Grummer, 1950; Lauderdale, Kirkpatrick, First, Hauser & Casida, 1965; Crighton & Lamming, 1969).

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*Present address: Department of Animal Science, Mississippi State University, Mississippi State, MS 39762, U.S.A.

Palmer, Teague & Venzke (1965a) measured the number and size of visible surface follicles > 2 mm in diameter of 20 second-parity sows slaughtered during 9 weeks of lactation. They found that the average diameter was greatest 1 day after parturition and during the 5th–9th weeks of lactation. The average number of follicles ⩾ 5 mm in diameter ranged from 0 to 5 during the first 4 weeks of lactation and then increased to more than 7 during Weeks 5–8 and to 13 during Week 9 (Fig. 1).
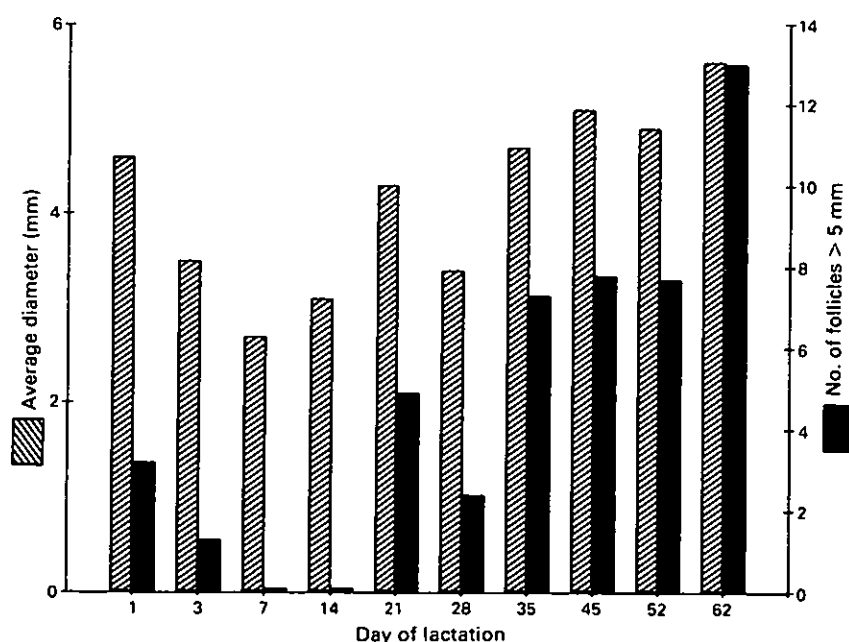

Fig. 1. Average diameter of visible surface follicles > 2 mm and number of follicles > 5 mm during lactation of sows. Each mean represents four sows; standard errors range from 0·2 to 0·8 for diameter and from 0 to 2·9 for number. After Palmer *et al.* (1965a).

Kunavongkrit, Einarsson & Settergren (1982) serially sectioned the ovaries of 13 primiparous sows slaughtered during 8 weeks of lactation. They counted all follicles ⩾ 1 mm in diameter and classified follicles as healthy or atretic on the basis of degeneration and pycnosis of the nuclei of granulosa cells. The percentage of follicles in the smallest-sized category (1–1·99 mm) decreased from 91 during the 1st week of lactation to 54 during the 8th week, and this was accompanied by a shift of follicles into the next two larger-sized categories (2–2·99 and 3–3·99 mm). Not more than 2% of follicles grew to a diameter > 4 mm during lactation (Fig. 2). The number of follicles ranged from 148 on Day 21 to 362 on Day 28 of lactation; however, the percentage of follicles classified as atretic declined from 64 on Day 4 to 41 on Day 56 (Fig. 3). Similarly, Palmer *et al.* (1965b) reported a higher rate of atresia in follicles examined in the 1st week *post partum* than in follicles examined during Weeks 2–9.

Weaning piglets on the day of birth (zero-weaned) removes the effect of suckling on secretion of gonadotrophins, but subsequent follicular development is often abnormal. For example, a high incidence of cystic follicles and prolonged oestrus in zero-weaned sows was reported by Peters, Short, First & Casida (1969b). Elliot, King & Robertson (1980) provided indirect evidence for aberrant ovarian function in zero-weaned sows because the farrowing-to-mating interval was 42 ± 26 (s.d.) days in zero-weaned sows compared with 35 ± 4 days for sows whose young were
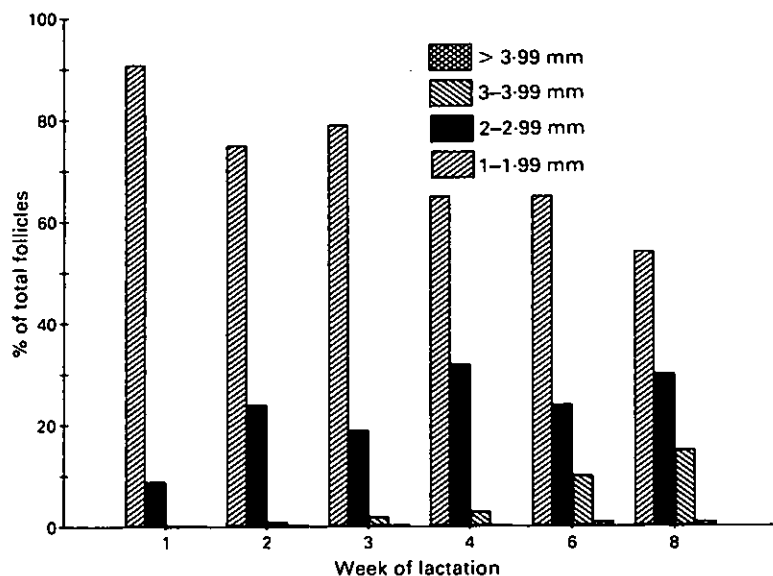
Fig. 2. Percentage of total follicles in various size categories during lactation of sows. Each mean represents 2 or 3 sows. After Kunavongkrit *et al.* (1982).
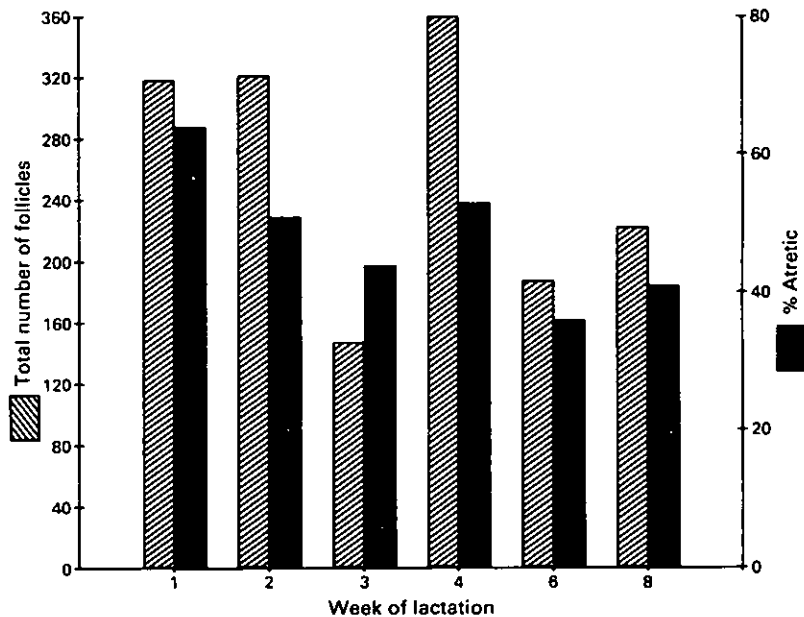

Fig. 3. Total number of follicles in serially sectioned ovaries and percentage of follicles classified as atretic during lactation of sows. Each mean represents 2 or 3 sows. After Kunavongkrit *et al.* (1982).

weaned on Day 30. Elliot *et al.* (1980) reported that most zero-weaned sows showed constant oestrus for 2 weeks *post partum*, and, based on blood progesterone levels, zero-weaned sows first ovulated 17 ± 7 days after parturition. Kunavongkrit, Kindahl, Einarsson & Edqvist (1983a) and Kunavongkrit, Edqvist & Einarsson (1983b) reported that 6 of 10 sows whose young were weaned at birth showed abnormal ovarian function during the next 6 weeks. They inspected the ovaries of these sows weekly by laparoscopy and observed that 4 sows developed ovarian follicular cysts 1–2 weeks *post partum*, one sow exhibited anovulatory oestrus 13–16 days *post partum* and one sow remained anoestrous for 42 days.

The number of follicles > 5 mm increases within 2–3 days after weaning. For example, Palmer *et al.* (1965a) reported an average of 12–14 surface follicles > 5 mm during the 4 days after weaning on Day 62 of lactation, and these values were higher than those observed during the first 8 weeks of lactation. The average diameter of follicles during the 4 days after weaning ranged from 6·0 to 7·6 mm and was higher than values reported during lactation (maximum of 5·6 mm). Cox & Britt (1982a) weaned litters at 35 days of lactation and observed a decline in the number of follicles < 5 mm in diameter from 82 at 0 h to 43 and 27 at 60 and 96 h, respectively. During this period, there was an increase in the number of follicles 5–10 mm in diameter (12, 27 and 17 at 0, 60 and 96 h, respectively) and they found 2·2 and 1·3 follicles > 10 mm in diameter at 60 and 96 h. Dyck (1983) measured follicles after weaning on Day 42 and adjusted values to the expected time of oestrus. He reported a decline in number of follicles < 4 mm and an increase in number of follicles 4–6 mm during Days 0 to 4 after weaning (Fig. 4). On day 6 after weaning, estimated to be about 12 h after onset of oestrus, he observed an average of 12 follicles > 6 mm and by approximately 1 day after ovulation there was 1 follicle 4–6 mm and no follicles > 6 mm.
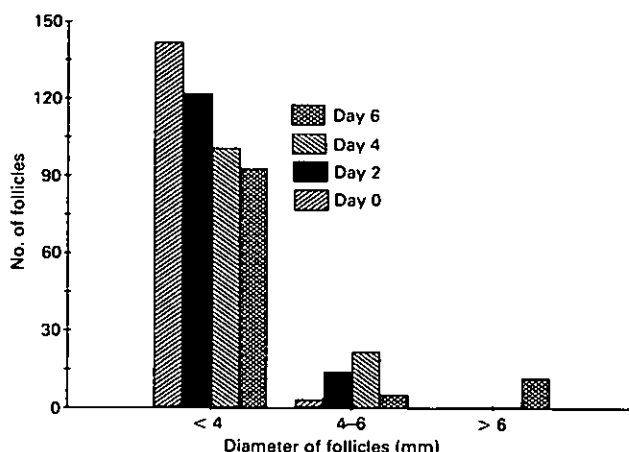

Fig. 4. Number of follicles of different sizes on Days 0, 2, 4 and 6 after weaning on Day 42 of lactation. Values were adjusted to time of expected oestrus after weaning; oestrus occurred an average of 5·5 days after weaning. Each mean represents 8–12 sows; standard errors ranged from 14 to 20 for follicles < 4 mm, 0·7 to 1·6 for follicles 4–6 mm and was 1·5 for follicles > 6 mm. After Dyck (1983).

Conclusions

The number of ovarian antral follicles does not change during lactation, but there is a gradual increase in the size of follicles and the greatest increase occurs after the 5th week. The percentage of follicles classified as atretic declines during lactation and this appears to be inversely related to the

percentage of follicles in the larger-sized categories. Weaning the litter on the day of birth leads to the formation of cystic follicles in about 30–50% of sows, apparently because of a failure of the positive-feedback mechanism to induce a release of LH (see next section). During lactations of up to 8 weeks duration, follicles seldom exceed 6 mm in diameter. Weaning results in a rapid increase in the number of medium- and large-sized follicles and a corresponding depletion of small-sized follicles. Presumably follicles that exceed 10 mm in diameter are healthy because there is a close correspondence between number of large-sized follicles at the onset of oestrus and the number of corpora lutea after ovulation.

Hormonal control of follicular development during and after lactation

Follicular growth during and after lactation is dependent on gonadotrophin secretion by the anterior pituitary; however, the exact roles which LH and FSH play in controlling follicular development have not been determined precisely. Substantial indirect evidence indicates that FSH stimulates development of follicles up to 5–6 mm whereas LH is necessary for final stages of follicle maturation and ovulation. There is also both direct and indirect evidence that the positive feedback response of LH to oestradiol may change during lactation and thus affect follicle maturation and ovulation.

Stevenson, Cox & Britt (1981) compared the concentrations of LH, FSH, total oestrogens and progesterone during and after lactation in intact sows and in sows ovariectomized within 4 days *post partum*. As FSH, but not LH, increased after ovariectomy, even though total oestrogens were unchanged, they proposed that FSH is controlled by some nonsteroidal factor (probably inhibin) secreted by the ovary. In contrast, they proposed that suckling of the litter was responsible for suppressing LH secretion, presumably by lowering secretion of gonadotrophin-releasing hormone (GnRH). Nevertheless, both serum LH and FSH increased beyond the 3rd week of lactation in intact and ovariectomized sows and this gradual increase in gonadotrophins during lactation may be related to a natural reduction in suckling frequency of the litter. Kunavongkrit (1984) reported that LH was higher during lactation in sows nursing small (2–4 pigs) litters than in sows nursing normal (7–12 pigs) litters. Bevers, Willemse, Kruip & van de Wiel (1981) demonstrated that the LH response to 25 µg synthetic GnRH increased from the 1st to the 2nd and from the 2nd to the 3rd week of lactation. The LH response to GnRH was not affected by the presence or absence of litters even though prolactin concentrations were 7-fold greater when young were present than when they had been separated from sows for 6 h before treatment with GnRH. When sows were treated with bromocriptine to suppress serum prolactin concentration, there was no effect on the LH response to GnRH. There is therefore little evidence that prolactin plays a role in the suckling-induced suppression of LH secretion or in the lower LH response to GnRH during early lactation.

Edwards & Foxcroft (1983a) were the first to demonstrate clearly that LH is released in discrete episodic pulses in some sows during lactation. In their study, samples were collected every 10 min for 6 h at selected times before and after weaning and in 5 of the 8 sows sampled during the 2 days before weaning at 3 or 5 weeks of lactation, LH was secreted in episodic pulses. Similarly, Shaw & Foxcroft (1985) collected samples every 15 min for 12 h before weaning at 3 weeks and detected an episodic LH pulse approximately every 2–5 h (Fig. 5).

The ability of oestradiol to stimulate a surge of LH apparently changes during lactation. For example, when Elsaesser & Parvizi (1980) challenged sows with oestradiol benzoate (60 µg/kg) on Day 5 of lactation, there was no evidence of a preovulatory surge of LH; however, treatment with oestradiol benzoate on Day 35 of lactation resulted in a significant increase in LH between 48 and 72 h after treatment and 4 of 9 treated sows ovulated. Ramirez, Bennett & Cox (1985a) challenged 13 lactating sows with 800 µg oestradiol benzoate at the beginning of the 2nd, 3rd or 4th week of lactation and observed an LH surge in one sow treated at the beginning of the 3rd week. Eight of 9 sows challenged during the 3rd or 4th weeks exhibited oestrus compared with 1 of 4 during the 2nd
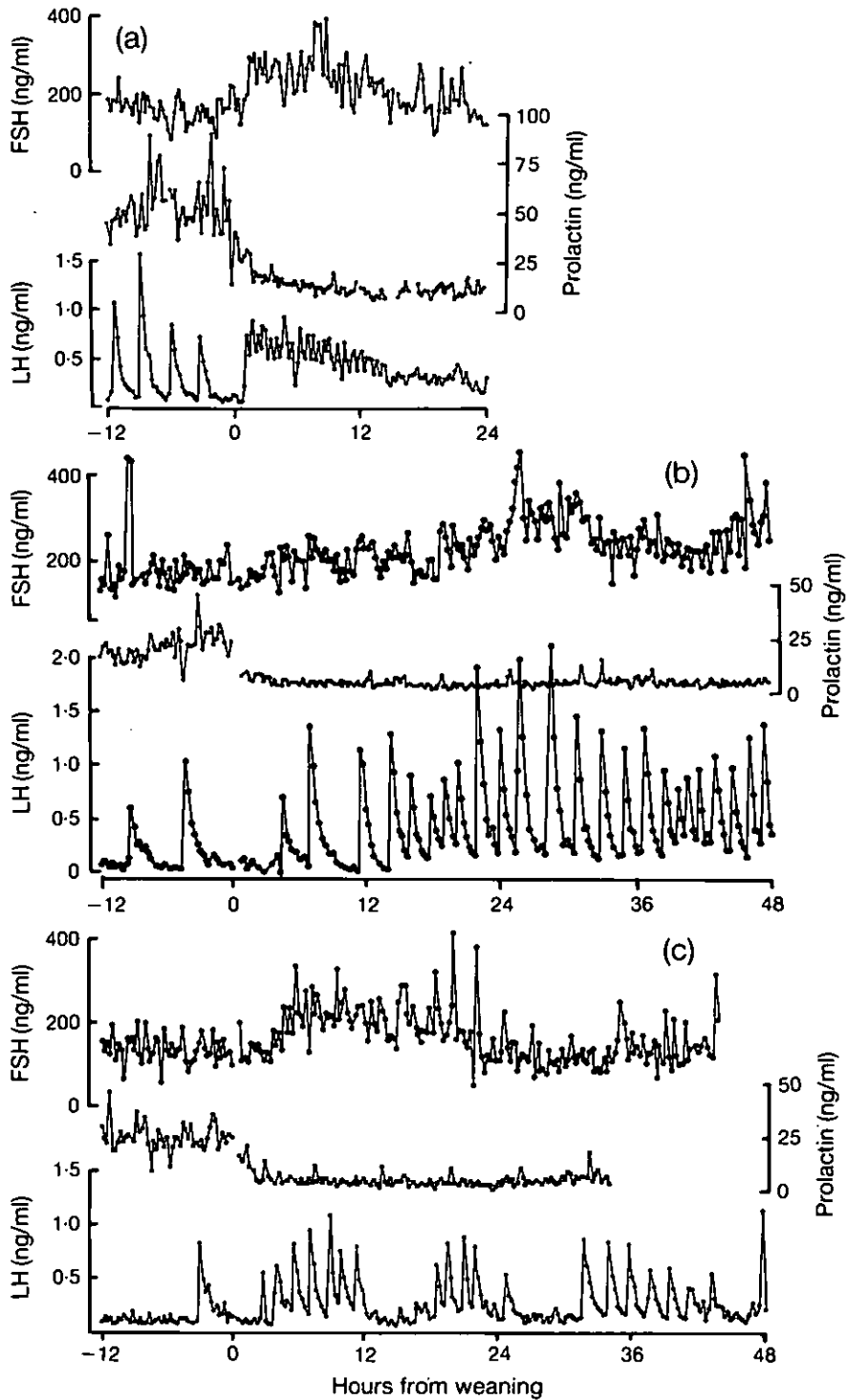
Fig. 5. Plasma LH, FSH and prolactin in sows weaned at 21 days *post partum* and with weaning to oestrus intervals of (a) 4 days, (b) 6 days and (c) > 11 days. (From Shaw & Foxcroft, 1985.)

week. Formation of cystic follicles in some zero-weaned sows (Peters *et al.*, 1969b; Elliot *et al.*, 1980; Kunavongkrit *et al.*, 1983a, b) may be related to this failure of the positive-feedback response of LH to oestradiol.

Weaning results in dramatic changes in hormone secretion and these changes also seem to be influenced by duration of lactation. Within 8–12 h after weaning, concentration of serum LH increases (Cox & Britt, 1982a; Edwards & Foxcroft, 1983a; Shaw & Foxcroft, 1985) and there is an increase in the frequency of episodic pulses of LH over the next 2–3 days (Cox & Britt, 1982c; Shaw & Foxcroft, 1985). Concentrations of FSH generally increase after weaning (Cox & Britt, 1982a; Edwards & Foxcroft, 1983a; Shaw & Foxcroft, 1985). However, the increase of FSH is not as great as for LH and there is no clear episodic pattern of secretion (see Fig. 6).

There are temporal relationships among concentrations of GnRH in the medial basal hypothalamus (MBH), stalk median eminence (SME) and hypophysial portal area (HPA) and concentrations of FSH and LH in the anterior pituitary and serum during the period from weaning to oestrus (Cox & Britt, 1982a). The concentration of GnRH in the MBH and SME increased by 60 h after weaning at 5 weeks and this was associated with an increase of LH, but not FSH, in the anterior pituitary (Fig. 6). By 96 h after weaning, GnRH was higher in MBH, SME and HPA compared with values at weaning (0 h), and this coincided with an increase in serum LH and FSH concentrations as part of the ascending portion of the preovulatory surge. A slight decline in LH content in the anterior pituitary occurred at 96 h, but pituitary FSH was unchanged.
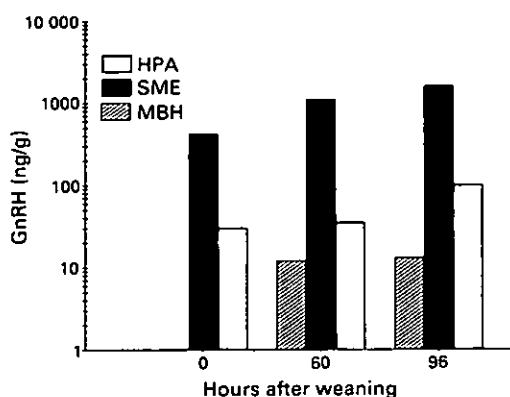

Fig. 6. Concentrations of GnRH in the medial basal hypothalamus (MBH), stalk median eminence (SME) and hypophysial portal area (HPA) after weaning on Day 35 of lactation. Each mean represents 9 sows. Note the logarithmic scale. After Cox & Britt (1982b).

Weaning of litters at 3 weeks compared with 5 weeks, resulted in lower levels of FSH 2–3 days after weaning (Edwards & Foxcroft, 1983a). Similarly, weaning early (10 or 21 days) compared with later (35 days) resulted in lower preovulatory surges of LH (Edwards & Foxcroft, 1983a; Kirkwood, Lapwood, Smith & Anderson, 1984a; Kirkwood, Lapwood, Smith, Moller & Garrick, 1984b).

Cox & Britt (1983) destroyed follicles >3 mm in diameter by electrocautery at 36 h before weaning on Day 35 of lactation. They observed that FSH, but not LH, increased significantly by 24 h after cauterization of follicles; however, there was no difference between sows subjected to cauterization of follicles and sham-operated controls in the levels of oestradiol-17β in serum. Moreover, the time from weaning to oestrus did not differ between treatment groups (3·4 and 3·6 days in cauterized and control sows, respectively). These observations provide additional evidence that an ovarian factor other than oestradiol-17β is involved in regulating the secretion of FSH and

that this factor is consistent with compensatory growth of small antral follicles to a mature preovulatory size within about 4 days.

There is a paucity of information about how hormones other than gonadotrophins and prolactin affect follicular development during and after lactation in sows. Kunavongkrit (1984) measured cortisol in zero-weaned sows and sows nursing small (2–6 pigs) or normal (7–9 pigs) litters. Cortisol values were higher during the 2 weeks after parturition in anovulatory zero-weaned sows than in those that ovulated within 2 weeks *post partum*. Concentrations of cortisol were not different between sows nursing small or normal litters, and levels in these sows were similar to those observed in anovulatory zero-weaned sows. Cortisol values declined about 20% from Day 1 to Day 14 *post partum* in lactating sows and in anovulatory zero-weaned sows. Zero-weaned sows that ovulated within 2 weeks *post partum* had a more rapid drop in cortisol concentration during the first 9 days after weaning, but then cortisol increased to levels comparable to values in anovulatory sows. Whether elevated concentrations of cortisol block the ability of oestradiol to induce a positive-feedback surge of LH during lactation remains to be determined. Adrenocorticotrophic hormone (ACTH) and high levels of corticoids will block LH secretion and ovulation in gilts and lead to the formation of cystic follicles (Liptrap, 1970, 1973; Barb, Kraeling, Rampacek, Fonda & Kiser, 1982).

Peters *et al.* (1968) and Peters, First & Casida (1969a) examined whether oxytocin treatment during early lactation affected follicular growth and levels of FSH and LH in the anterior pituitary. In their first study (Peters *et al.*, 1968), sows whose litters were weaned on Day 6 were given 10 units of oxytocin every 2 h from Days 6 to 13 of lactation. Oxytocin did not affect pituitary levels of LH or FSH or follicular development compared with values for nonsuckling controls. Suckling sows had higher levels of pituitary FSH and less follicular development on Day 13 *post partum* than did control or oxytocin-treated nonsuckling sows. In the second experiment, Peters *et al.* (1969a) gave 20 units of oxytocin every 2 h from Day 1 to Day 7 of lactation to intact or mammillectomized sows in the presence or absence of piglets. Oxytocin depressed follicular fluid weight in intact and mammillectomized sows when piglets were present, but not when young were absent. Intact sows given oxytocin had more pituitary FSH than did oxytocin-treated mammillectomized sows. Ellendorff (1984) presented preliminary evidence that administration of intravenous pulses of oxytocin, which mimicked the suckling-induced release of oxytocin, delayed oestrus for at least 3 weeks after weaning in sows but he did not report whether oxytocin blocked the increase in LH after weaning or whether sows ovulated without expressing oestrus.

Conclusions

Mechanisms responsible for controlling secretion of LH and FSH during and after lactation differ in several respects. Secretion of LH is apparently controlled primarily by secretion of GnRH, and suckling suppresses LH through limiting synthesis and secretion of GnRH. The ability of GnRH to induce LH release increases during lactation, possibly because of an increase in GnRH receptors in the pituitary as lactation progresses. Secretion of FSH depends in part on some ovarian factor other than oestradiol and in part on secretion of GnRH. The ability of oestradiol to induce a surge of LH increases beyond the 3rd week of lactation. Weaning leads to an increase in synthesis and secretion of GnRH and a corresponding increase in LH, but not FSH.

Oxytocin, ACTH and adrenal corticoids may affect follicular development, but the mechanisms whereby these effects are manifested remain to be determined. Indirect evidence suggests that oxytocin may affect follicular development through an effect on secretion of FSH whereas ACTH and adrenal corticoids may block secretion of LH.

Stimulation of follicular development in anoestrous sows

Administration of gonadotrophins, GnRH or oestradiol stimulates oestrus and ovulation in

anoestrous sows; however, in lactating sows, the response is affected by the duration of lactation. Ovulation rate and fertility vary greatly among treatments, probably because of the amount of follicular development that occurs in response to treatments.

Peters *et al.* (1968) gave sows 20 mg of a crude FSH preparation per day from Days 8 to 11 *post partum*. Half of the sows had been hysterectomized on Day 6 *post partum* and all sows were slaughtered on Day 13. Treatment with FSH stimulated a 6-fold increase in follicular fluid weight and FSH-treated sows had an average of 18 ovulations at slaughter compared with zero ovulations in untreated sows. Intact sows given FSH had three times as many ovulations as did hysterectomized sows. In a subsequent study, Peters *et al.* (1969b) conducted three experiments in an attempt to induce fertility in post-partum sows. In the first experiment, they gave sows 25 mg of a crude FSH preparation per day for 3 days beginning on Day 6 or 21 of lactation. On the 5th day of treatment, FSH-treated sows received 52 mg bovine pituitary extract. Sows were slaughtered 7 days after the beginning of treatment with FSH. Sows treated early (beginning on Day 6) had 8 corpora lutea (CL) and 14 follicles > 4 mm compared with 15 CL and 28 follicles in sows treated later. However, no fertilized ova were recovered from sows treated with gonadotrophin beginning on Days 6 and 21. In a second experiment, sows were zero-weaned or allowed to nurse litters, and beginning on Day 1 *post partum*, were given the same gonadotrophin treatment as in the first experiment. Suckling sows had a higher percentage of ovarian structures that were new CL than did weaned sows (44 *vs* 20%). In a third experiment, sows were again given the same treatment regimen and, in contrast to results obtained in the first experiment, sows treated early had more CL (26) than sows treated later (13), but sows treated later had more follicles > 4 mm than sows treated early (41 *vs* 16). Less than 2% of ova recovered from the early group were fertilized compared with 22% in the late group.

Pregnant mare's serum gonadotrophin (PMSG or horse CG) alone or in combination with human choronic gonadotrophin (hCG) has been used extensively to induce follicular development and ovulation during lactation. A summary of results from several experiments is presented in Table 1. In general, oestrus and conception cannot be induced successfully during the first 5 days of lactation. There appears to be an increase in the percentage of sows that exhibited oestrus after the 4th week of lactation, but data are limited during the first 4 weeks. Beyond the 3rd week *post partum* there is a clear increase in the percentage of sows that farrow to inseminations at the induced oestrus.

Table 1. Summary of studies on induction of follicular development in lactating sows with pregnant mares' serum gonadotrophin (PMSG)

Day of lactation	Dosage of PMSG (i.u.)	No. exhibiting oestrus/ no. treated (%)	No. farrowing/ no. treated (%)	References
0–5	700–1500	1/7 (14)	0/17 (0)	Cole & Hughes (1946); Hausler *et al.* (1980)
7–13	1500	NR	5/18 (28)	Hausler *et al.* (1980); Guthrie *et al.* (1978)
14–20	1000–2600	4/6 (67)	31/63 (49)	Hausler *et al.* (1980); Guthrie *et al.* (1978); Hodson *et al.* (1981); Heitman & Cole (1956)
21–29	1000–3000	3/9 (33)	108/169 (64)	Cole & Hughes (1946); Guthrie *et al.* (1978); Hodson *et al.* (1981); Heitman & Cole (1956); Crighton (1970)
30–36	750–3400	28/38 (74)	73/114 (64)	Cole & Hughes (1946); Hodson *et al.* (1981); Heitman & Cole (1956)
> 36	450–3400	78/89 (88)	77/107 (72)	Cole & Hughes (1946); Hodson *et al.* (1981); Heitman & Cole (1956)

NR = not recorded.

Cox & Britt (1982b) were the first to demonstrate that fertile oestrus could be induced in multiparous lactating sows by pulsatile administration of GnRH (see Table 2). They administered 2·5 µg GnRH intravenously every 2 h or 1·5 µg every h and treatments began on Day 25 (every 2 h) or 31 (hourly) of lactation. Three of 6 sows given GnRH every 2 h and 6 of 6 given GnRH hourly exhibited oestrus during lactation; however, 0 of 10 control sows showed oestrus until after litters were weaned. Oestrus occurred 96 (2 hourly) and 91 (hourly) h after onset of GnRH pulses. In all cases, GnRH treatment continued for 24 h after the onset of oestrus. In a subsequent study, Ramirez, Cox & Bennett (1985b) gave hourly pulses of 1·5 µg GnRH to 10 primiparous sows beginning on Day 24 of lactation. Half of the sows received hourly pulses until 24 h after onset of oestrus, whereas pulsing was stopped in the remaining sows at the onset of oestrus. Onset of oestrus occurred 123 h after initiation of GnRH pulses. The preovulatory LH peak was higher in sows pulsed for 24 h after the onset of oestrus than for sows in which pulsing was stopped (2·5 ± 0·3 *vs* 1·9 ± 0·3 ng/ml), but ovulation rate (17 *vs* 18) and subsequent litter size 12 *vs* 10) did not differ between groups. Hourly pulses of 2·0 µg GnRH were given to lactating primiparous sows during the spring (March and April) or late summer (August) to determine whether the season of year affected the response to GnRH (J. H. Britt, J. D. Armstrong & K. L. Esbenshade, unpublished observations). Pulsing began earlier during lactation than in previous studies (Day 13 ± 3 during spring and Day 17 ± 4 during summer). Three of 6 sows treated during spring exhibited oestrus within 7 days compared with 3 of 4 during summer. Although number of sows treated was limited, it appeared that season did not affect response, but the overall lower response, compared with our previous studies conducted during later stages of lactation, may indicate that stage of lactation affects the response to GnRH. During the summer, 4 additional sows received continuous intravenous infusions of GnRH via a subcutaneous osmotic pump with an infusion rate of 2·5 µg/h for 9 days. None of these sows exhibited oestrus during lactation, but 3 of 4 were in oestrus within 8 days after weaning (6 days after removal of pumps).

Table 2. Summary of trials on induction of follicular development and oestrus in anoestrous sows by pulsatile administration of GnRH

Physiological state	Parity	Dose and frequency of GnRH*	No. in oestrus/ no. treated (%)	Hours to oestrus	Reference
Lactation, Day 25	>1	2·5 µg/2 h	3/6 (50)	96	Cox & Britt (1982b)
Lactation, Day 31	>1	1·5 µg/h	6/6 (100)	91	Cox & Britt (1982b)
Lactation, Day 24	1	1·5 µg/h	10/10 (100)	123	Ramirez *et al.* (1985b)
Lactation, Day 13	1	2·0 µg/h	3/6 (50)	125	J. H. Britt, J. D. Armstrong & K. L. Esbenshade, unpublished
Lactation, Day 17	1	2·0 µg/h	3/4 (75)	128	J. H. Britt, J. D. Armstrong & K. L. Esbenshade, unpublished
Postweaning, Day 30†	1	1·5 µg/h	4/4 (100)	84	Armstrong & Britt (1985)

* GnRH was administered as discrete intravenous pulses every h or 2 h.
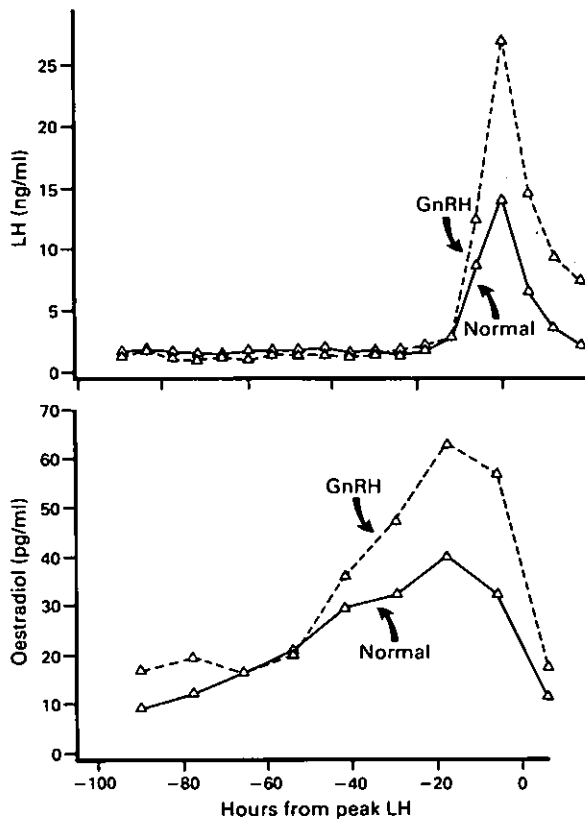† Sows were anoestrous for 30 days after weaning.

Fig. 7. Concentrations of LH and oestradiol in normal sows that exhibited spontaneous oestrus after weaning and in chronically anoestrous sows given hourly pulses (1·5 µg) of GnRH beginning 30 days after weaning. Values are plotted in relation to the LH peak. Standard errors ranged from 0·1 to 6·1 for LH and from 2·2 to 8·0 for oestradiol and in both cases were proportional to the mean. From Armstrong & Britt (1985).

Postweaning anoestrus delays remating in sows and its occurrence is greater in primiparous sows and sows weaned during summer and early autumn (Love, 1978; Stork, 1979; Hurtgen, Leman & Crabo, 1980; Cox, Britt, Armstrong & Alhusen, 1983b; Britt, Szarek & Levis, 1983). Ovaries of the chronically anoestrous sow have few medium- to large-sized follicles (Cox, Esbenshade & Britt, 1983a). Oestrus and ovulation can be stimulated in weaned anoestrous sows by treatment with PMSG alone or in combination with hCG (Schilling & Cerne, 1972; Dyck, Palmer & Simaraks, 1979; King, Williams & Barker, 1982; Dial, BeVier, Hixson & Gustafsson, 1984), by treatment with hCG alone (Dial *et al.*, 1984), by oestradiol alone or in combination with progesterone (Dyck *et al.*, 1979; Cox *et al.*, 1983a; Dial *et al.*, 1984) and by hourly pulses of GnRH (Armstrong & Britt, 1985; Fig. 7). Normal fertility after such treatments has only been reported for sows treated with PMSG alone or in combination with hCG or in sows given hourly pulses of GnRH. Apparently the other treatments are ineffective in inducing fertile oestrus because they do not promote additional follicular development. For example, oestradiol benzoate will induce an LH surge in anoestrous sows, but the subsequent increase in progesterone is lower than values observed during a normal oestrous cycle or after postweaning oestrus (Cox *et al.*, 1983a; Dial *et al.*, 1984). The LH surge induced by oestradiol benzoate apparently causes ovulation of only those few mature follicles present in the ovaries at treatment.

Oestradiol benzoate has been given 1–2 days after weaning in an attempt to overcome the lower fertility common after short lactations. Treatment with oestradiol benzoate has not proved very successful because ovulation rates in oestradiol-treated sows were lower than expected (Edwards & Foxcroft, 1983b; Kirkwood *et al.*, 1984b). Administration of PMSG 1 day after weaning greatly reduces postweaning anoestrus in primiparous sows weaned at 3–4 weeks (Hurtgen & Leman, 1979; Britt, Esbenshade & Heller, 1984).

Conclusions

Follicular development, oestrus and ovulation can be stimulated during lactational or post-weaning anoestrus by administration of various hormonal regimens. The most successful treatments are those which stimulate sufficient follicular development so that endogenous secretion of oestrogen leads to a positive feedback surge of LH. Thus administration of PMSG or PMSG plus hCG, or administration of hourly pulses of GnRH promotes follicular development, oestrus and a normal ovulation rate in anoestrous sows. The PMSG or PMSG + hCG treatments are more convenient because only one or two injections are required compared to 60 or more hourly injections when pulses of GnRH are given.

Managemental and environmental factors that affect follicular development during and after lactation

Occurrence of oestrus during lactation or after weaning is affected by several factors including nutrition, suckling intensity of the litter, season, parity and exposure to boars. Presumably these factors affect the occurrence of oestrus through an effect on follicular development.

Nutrition

Energy intake during lactation affects the weight change of the sow during lactation and weight at weaning. Sows that lose less weight during lactation rebreed sooner after weaning than those that have greater weight losses (Etienne & Duee, 1976; Lengele, 1978; Miyajima, Shiiba, Kohno & Inagaki, 1979; van der Heyde, Lievans & Calus, 1980; Den Hartog & van der Steen, 1981; Cox *et al.*, 1982; Armstrong & Britt, 1984). The effects of different energy (Reese *et al.*, 1982; Reese, Peo & Lewis, 1984) or feed (King & Williams, 1984a) intakes on weight and backfat changes during lactation and the occurrence of postweaning oestrus have been examined. Inadequate intakes of energy prolong the interval from weaning to oestrus. It appears that intakes of about 50 MJ/day (approximately 4 kg concentrate) during lactation are needed for satisfactory follicular development after weaning.

Protein intakes during lactation also affect ovarian activity (Svajgr *et al.*, 1972; O'Grady & Hanrahan, 1975; King & Williams, 1984b). Table 3 illustrates the effect of both protein and energy intake during lactation on the performance of primiparous sows. It is clear that a deficiency of either protein or energy during lactation leads to greater weight losses during lactation and less follicular development after weaning. Gilts deprived of adequate protein intake during first gestation (2% crude protein) and lactation (5% crude protein) failed to recycle by 35 days after weaning (Svajgr *et al.*, 1972); however, when these primiparous sows were given PMSG (1500 i.u.) followed 90 h later by hCG (750 i.u.) they exhibited oestrus 12–36 h after hCG and had an average of 15 CL by 6 days after hCG injection.

The effects of feed intake after weaning on the occurrence of oestrus seem to differ between primiparous and multiparous sows. In general, increasing feed intake after weaning was not beneficial in reducing the interval from weaning to oestrus in multiparous sows (Dyck, 1972; Brooks, Cole, Rowlinson, Croxson & Luscombe, 1975; Fahmy & Dufour, 1976; Tribble & Orr, 1982). However, the remating interval of primiparous sows was improved in some studies by increasing

Table 3. Effect of energy and protein intake during lactation on performance of primiparous sows*

	Dietary treatment†			
	High energy, high protein	High energy, low protein	Low energy, high protein	Low energy, low protein
No. of sows	17	17	17	17
Weight change during lactation, kg	−3·9	−32·5	−29·8	−35·4
Backfat change during lactation, mm	0·3	−1·4	−7·2	−5·4
Daily nitrogen balance, g	7·6	−13·1	−13·2	−19·0
% in oestrus within 8 days after weaning	88	53	53	53
Weaning-to-oestrus interval, days	6·9	18·5	15·3	21·5

* After King & Williams (1984b).
† High energy = 54−59 MJ/day; low energy = 25−29 MJ/day; high protein = 550−750 g/day; low protein = 300−320 g/day.

feed intake after weaning (Brooks & Cole, 1972) or by supplementing rations with 10% fat during summer when the remating performance of control sows was low (Cox *et al.*, 1983b). However, in other studies (King & Williams, 1984a) reproductive performance of primiparous sows was not improved by increased energy intake after weaning. The response may depend on whether remating rate in controls is impaired, because Cox *et al.* (1983b) reported that supplementation of rations with 10% fat was not beneficial during winter when control sows mated again on schedule.

Suckling intensity

An inverse relationship exists between suckling intensity and follicular development. Fahmy, Holtman & Baker (1979) reported that the interval from weaning to oestrus was negatively related with number of piglets nursed. Older piglets suck less frequently, and so the interval from weaning to oestrus decreases with longer lactations (Self & Grummer, 1958; Moody & Speer, 1971; Cole, Varley & Hughes, 1975).

Suckling intensity can be altered by separating piglets from sows for various periods each day (partial weaning) or by weaning a portion of the litter early (split weaning). Partial weaning for 6–12 h daily beginning the 2nd–3rd week of lactation resulted in oestrus during lactation in a high percentage of sows in most studies (Smith, 1961; Walker & England, 1978; Thompson, Hanford & Jensen, 1981; Stevenson & Davis, 1984) but not in all (Kirkwood, Smith & Lapwood, 1983; Henderson & Hughes, 1984). Partial weaning for 2 days before weaning improved remating performance when performance of control sows was poor, but not when control sows mated again at the expected time (Britt & Levis, 1982).

Split weaning usually involves an abrupt reduction in litter size before final weaning (Stevenson & Britt, 1981), typically by weaning the larger piglets of a litter 2–5 days before weaning the smaller piglets (Cox *et al.*, 1983b; Stevenson & Davis, 1984), and increases the percentage of sows exhibiting oestrus by 5–10 days after weaning.

Kunavongkrit (1984) allowed primiparous sows to nurse 7–12 piglets (normal litters) for 3 or 5 weeks or 2–4 piglets (small litters) for 5 weeks. The interval from weaning to oestrus was 11 and 8 days for sows nursing normal litters and weaned at 3 or 5 weeks, respectively, and there was no difference in the proportion of sows exhibiting oestrus by 3 weeks after weaning. Sows nursing small litters for 5 weeks exhibited oestrus 6 days after weaning.

Season and parity

Although the pig is not normally considered to be a seasonal breeder, there is clear evidence that season affects reproductive performance (Mauget, 1982). In general there appears to be a delay in onset of oestrus after weaning when litters are weaned during summer or early autumn and this delay is greater in primiparous than multiparous sows (Aumaitre, Dagorn, Legault & LeDenmat, 1976; Love, 1978; Stork, 1979; Hurtgen *et al.*, 1980; Karlberg, 1980; Benjaminsen & Karlberg, 1981; Britt *et al.*, 1983; Stevenson, Pollmann, Davis & Murphy, 1983).

Armstrong, Britt & Cox (1984) measured GnRH in the hypothalamus, LH and FSH in anterior pituitaries and serum, follicular development, and the secretion of oestrogen in primiparous sows fed *ad libitum* during lactation and weaned 24 days *post partum* in March or September. The interval from weaning to oestrus was longer for sows weaned during September (224 h) than for sows weaned during March (93 h). Sows weaned during September had lower feed intakes during lactation, lower levels of GnRH in the MBH, SME and HPA at 0 and 72 h after weaning and lower levels of LH and FSH in the anterior pituitary at these times. About half of the sows weaned during September had atypical patterns of oestradiol secretion after weaning; periods of transient increases of oestradiol in plasma occurred during the 10 days after weaning without inducing surges of LH. There were therefore distinct differences between seasons in postweaning endocrine changes in sows subjected to normal seasonal variations in photoperiod, maximum ambient temperature and feed intake.

Effects of photoperiod during lactation on remating performance are unclear. Mabry, Cunningham, Kraeling & Rampacek (1982) reported that the same proportion of sows exposed to long (16L:8D) or short (8L:16D) photoperiods returned to oestrus and had similar weaning to oestrus intervals. In contrast, Stevenson *et al.* (1983) found that a greater proportion of sows given a long (16L:8D) photoperiod returned to oestrus within 5 days of weaning compared with sows given an extremely short (1L:23D) photoperiod (83 *vs* 68%); however, the average interval to oestrus was unaffected. Perera & Hacker (1984) exposed weaned sows to one of three photoperiods (24L:0D; 12L:12D; 0L:24D) from weaning to oestrus. The interval to oestrus was unaffected, but sows exposed to the longest photoperiod (24L:0D) exhibited oestrus for a longer period (4 days) than did those exposed to the other two photoperiods (2·7 days).

Exposure to boars and grouping of sows

The boar produces pheromones that stimulate oestrous activity in gilts and sows. Exposure of lactating sows to a synthetic boar pheromone (5α-androst-16-en-3-one) or to mature boars reduced the interval from weaning to oestrus (Hillyer, 1976; Petchey & English, 1980). Several studies have shown that oestrus occurred during lactation when sows and their litters were grouped, beginning 2–3 weeks *post partum*, and given continual exposure to boars (Rowlinson, Boughton & Bryant, 1975; Petchey & Jolly, 1979; Rowlinson & Bryant, 1981, 1982a, b; Bryant, Palmer, Petherick & Rowlinson, 1983; Bryant & Rowlinson, 1984). Others (Guthrie, Pursel & Frobish, 1978; Petchey, Dodsworth & English, 1978) failed to observe a stimulatory effect of grouping and boar exposure on the expression of oestrus during lactation. In one report (Petherick, Rowlinson & Bryant, 1977), grouping of sows and litters resulted in lactational oestrus when the boar was not present. Booman, van de Wiel & Jansen (1983) observed that exposure to boars tended to stimulate secretion of LH in weaned anoestrous sows.

Conclusions

Several environmental or managemental factors affect the occurrence of oestrus during lactation or after weaning. Presumably these factors affect follicular development through an effect on gonadotrophin secretion, but the possibility of a direct effect on the ovary cannot be excluded

on the basis of data currently available. An understanding of the mechanisms whereby these factors affect follicular development is important for the development of an optimum environment and management for sows during and after lactation.

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