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J Anim Sci 2001. 79:176-187.

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Endocrine relationships of Meishan and White composite females after weaning and during the luteal phase of the estrous cycle¹

T. Wise^{2,3}, J. Klindt, H. J. Howard⁴, A. J. Conley⁵, and J. J. Ford

USDA, ARS, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933-0166

ABSTRACT: Endocrine differences between European crossbred and Chinese Meishan females have been somewhat modest. Indwelling jugular cannulas were placed in Meishan (n = 7) and White composite (n = 6) multiparous sows before weaning, and blood was sampled from 4 h before to 240 h after removal of litters. Temporal changes in FSH, triiodothyronine (T₃), and tetraiodothyronine (T₄) after weaning differed between Meishan and White composite sows. Plasma cortisol concentrations were higher in Meishan sows than in White composite sows ($P < 0.01$), but there were no temporal differences between breeds after weaning. Other hormones monitored (prolactin, GH, IGF-I, and inhibin) were not different between breeds. In the second experiment, Meishan gilts (n = 7) and sows (n = 7) and White composite sows (n = 9) were cannulated during the luteal phase of the estrous cycle and sampled after treatments consisting of GnRH (15 and 150 ng/kg BW), ovariectomy, estradiol cypionate challenge after ovariectomy (10 µg/kg BW), and GnRH antagonist. In response to GnRH challenge, White composite sows had

elevated ($P < 0.05$) concentrations of gonadotropins compared with Meishan. Cortisol concentrations were elevated in Meishan as compared with White composite females ($P < 0.01$) but unaffected by GnRH treatment. After ovariectomy, LH concentrations increased 3 h sooner in White composite than in Meishan females. After GnRH antagonist, declines in gonadotropins were comparable in both breeds, but LH increased in Meishan females by 20 h but not until after 54 h in White composite females. White composite females demonstrated only a short decline in FSH in response to the GnRH antagonist, but Meishan females had a prolonged decline in FSH concentrations. Consistently elevated cortisol concentrations in Meishan females may positively impact ovarian function; thus, the assumption that high plasma cortisol concentration as an index of stress that impairs reproductive function should be reevaluated in swine. There were few endocrine differences that would relate to or explain increased ovulation rates found in the Meishan breed; thus, other mechanisms must exist to explain the increase in ovarian function in the Meishan breed.

Key Words: FSH, Hydrocortisone, LH, Meishan, Ovulation Rate, Pigs

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J. Anim. Sci. 2001. 79:176–187

Introduction

Although ovulation rate and litter size are greater in Chinese Meishan than in European crossbred females, the mechanism responsible for these economical traits is unelucidated. Differences in ovulation rate between Meishan and White composite females increase with

age (Christenson, 1993). Few differences in concentrations of gonadotropins are noted between these breeds (Hunter et al., 1994, 1996; Miller et al., 1998); however, with GnRH challenge, European crossbred females have a greater release of gonadotropins than Meishans (Tilton et al., 1994). These findings are indicative of differential sensitivity to GnRH.

Generally increased cortisol concentrations are associated with stress, resulting in decreased reproductive efficiency in farm animals, but this concept is undergoing new evaluation. Cortisol, in rats, can increase the pituitary content of FSH, FSH β -subunit mRNA, and

¹Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

²We thank USDA/NIDDKD for FSH antisera, FSH, and LH reference preparations and oFSH for iodinations; A. F. Parlow for LH antisera and pLH for iodination; Swine Operations Personnel for care of the animals; and S. Hassler, M. Judy, A. Kruger, and L. Parnell for technical assistance.

Received April 7, 2000.

Accepted August 18, 2000.

³Correspondence: P.O. Box 166 (phone: 402-762-4185; fax: 402-762-4382; E-mail: wise@email.marc.usda.gov).

⁴Present address: Center for Veterinary Medicine, Food and Drug Administration, HFV-126, 7500 Standish Place, Rockville, MD 20855.

⁵Present address: Department of Population Health and Reproduction, University of California-Davis, Davis, CA 95616.

serum FSH bioactivity (McAndrews et al., 1994; Kilen et al., 1996). Cortisol receptors are found on granulosa cells (Tetsuka et al., 1999), and the synergism of corticoids with FSH and insulin to increase granulosa cell steroidogenesis indicates a possible role for corticoids in ovarian function (Adashi et al., 1981; Spicer and Chamberlain, 1998; Barkan et al., 1999). The objectives of this study were to 1) compare secretion of reproductive and metabolic hormones of Meishan and White composite sows during follicular development after weaning that may relate to differences in ovulation rates of these two breeds, 2) determine whether different levels of sensitivity of pituitary function exist in Meishan and White composite females in response to GnRH, ovariectomy, or GnRH antagonist, and 3) compare plasma cortisol concentrations in Meishan and White composite females after weaning and after GnRH challenge. Cortisol was a primary interest because Meishan boars have greater plasma cortisol concentrations than White composite boars (Wise et al., 2000).

Materials and Methods

Multiparous White composite ($\frac{1}{4}$ Yorkshire \times $\frac{1}{4}$ Landrace \times $\frac{1}{4}$ Large White \times $\frac{1}{4}$ Chester White; $n = 6$) and Chinese Meishan ($n = 7$) sows were monitored for endocrine differences associated with resumption of follicular development and ovulation after weaning. Live piglets born to Meishans were 12.6 ± 0.6 and 10.3 ± 0.7 for White composite sows. Piglet numbers were adjusted to 10 per sow within 48 h after parturition and weaned at d 28 to 32 of lactation. Lactating animals were catheterized (jugular) 4 d prior to weaning. Sows were bled 4 h and 2 h before weaning, then every 3 h for 18 h, and thereafter (18 h after weaning) every 6 h to 10.5 d after weaning. Occurrence of estrus was determined by twice daily visual observation in the presence of a boar. Sows were slaughtered during the luteal phase and number of corpora lutea counted.

In a second experiment, White composite sows ($n = 9$; 411.5 d of age; first parity), Meishan gilts ($n = 7$; 234.6 d of age), and Meishan sows ($n = 7$; 591.0 d of age; second parity) were cannulated (jugular vein) during the early luteal phase (d 3 to 8 of the estrous cycle) and tested for differential pituitary function. Blood samples were taken at 20-min intervals for 120 min for a pretreatment control period. GnRH was then administered (15 and 150 ng/kg BW on d 9.6 ± 0.4 and 10.6 ± 0.4 , respectively, of the estrous cycle) via the jugular cannula followed by flushing with saline. After GnRH administration, animals were bled at 10-min intervals for 30 min and then at 20-min intervals for 3.5 h. The dose of 15 ng/kg BW of GnRH was selected as the minimum dose to elicit an increase in FSH to test for possible breed differences in sensitivity to GnRH.

Possible differences in pituitary sensitivities to gonadal feedback were evaluated in the above females after collection of two blood samples 30 min apart followed by ovariectomy on d 12.4 ± 0.4 of the estrous

cycle. Anaesthesia was induced with Telazol (Fort Dodge Laboratories, Fort Dodge, IA) and maintained with closed-circuit halothane (Halocarbon Laboratories, River Edge, NY) and oxygen. Animals were then bled at 3, 6, 12, 24, 36, 48, 72, 120, 168, 264, and 336 h after ovariectomy. Two weeks after ovariectomy, estradiol cypionate (ECP; 10 μ g/kg BW; Upjohn, Kalamazoo, MI) was administered and blood samples were collected at 0, 1, 2, 4, 6, 9, 12, 24, 36, and 48 h after injection. After ovariectomy, gonadotropins are considerably increased: thus, a trial using a GnRH antagonist was begun to test for differential pituitary sensitivity in the two breeds of swine. The GnRH antagonist (Centrorelis SB-75, Dept. Biochem., Univ. Nebraska, Lincoln; 2, 10, or 50 μ g/kg BW; Zanella et al., 2000) was administered 9 d after ECP treatment, and animals were bled at 0, 1, 3, 6, 12, 24, 52, and 96 h after GnRH antagonist injection. Procedure for handling pigs complied with those specified in the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (FASS, 1999).

Assays

All blood samples were refrigerated immediately after collection; after centrifugation, plasma was stored at -20°C . In the first experiment, plasma was analyzed for prolactin (Klindt and Stone, 1984), GH (Klindt et al., 1983), IGF-I (Houseknecht et al., 1988; Howard and Ford, 1992), LH (Zanella et al., 2000), FSH (Ford et al., 1997), inhibin (Schanbacher, 1988; Trout et al., 1992), progesterone (Wise et al., 1991), estradiol (Ford, 1983), and cortisol (Wise et al., 2000). The interassay CV for the assays of prolactin, GH, IGF-I, LH, FSH, inhibin, progesterone, estradiol, and cortisol were 13, 11, 13, 10, 17, 13, 12, 20, and 9%, respectively. The limit of assay sensitivity for prolactin, GH, IGF-I, LH, and FSH was 2, 1, 0.2, 0.3, and 4 ng/mL, respectively. Triiodothyronine (T_3) and tetraiodothyronine (T_4) were measured in sow plasma (50 and 25 μ L, respectively) with RIA kits supplied by Diagnostic Systems Laboratories, Inc. (Webster, TX). Limits of assay sensitivity were 25 and 250 pg/tube for T_3 and T_4 , respectively. Interassay variation for the T_3 and T_4 assay were 3.2 and 2%, respectively. In the second experiment, plasma samples were assayed for LH, FSH, and cortisol (GnRH challenges).

Statistical Analysis

Hormonal data for breed differences after weaning were analyzed with the split-plot model of GLM (Data Desk⁴, Data Descriptions, Inc., Ithaca, NY) and included animal, breed, time after weaning, and time \times breed interaction. Postweaning reproductive hormones were synchronized to the postweaning FSH peak associated with estrus. In experiments in which females were injected with GnRH, estradiol, or GnRH antagonist, each female acted as its own control (pretreatment concentrations; paired *t*-test; Snedecor and Cochran, 1974).

After pretreatment and postinjection responses were analyzed, differences in slopes of responses and declines from peak concentrations were monitored by developing regression lines from a GLM analysis that included animal, breed, time, and breed \times time interaction. Testing for differences of slopes between breeds was also by GLM procedure and means comparisons by LSD.

Results

Postweaning Endocrine Changes

Ovulation rate was 20.1 ± 0.8 vs 18.6 ± 2.0 for Meishan and White composite sows, but one White composite sow had an unusual 28 ovulations (without this White composite sow, ovulation rate was more representative; 20.1 ± 0.8 vs 16.8 ± 0.6 ; $P < 0.01$ for Meishan and White composite, respectively). Interval from weaning to the preovulatory gonadotropin surge was shorter for Meishan than for White composite sows (54.8 vs 100.4 h after weaning, respectively; $P < 0.02$). The interval from estrus to the ovulatory gonadotropin surge was similar in both breeds (5.5 ± 5 h).

Changes in GH and prolactin were not different ($P < 0.1$) between Meishan and White composite sows (Figure 1). Prolactin concentrations quickly declined ($P < 0.01$) after weaning (Figure 1a). No differences were noted in the levels or day trends after weaning for T_3 (Figure 2a) between Meishan or White composite sows. Concentrations of T_3 increased after weaning for both breeds. Whereas T_3 concentrations increased and plateaued after weaning in Meishan gilts, T_3 concentrations increased and then declined in White composite sows ($P < 0.01$). Concentrations of T_4 were not different between breeds, but T_4 levels followed trends of T_3 in Meishan sows and were inverse to T_3 in White composite sows ($P < 0.05$; Figure 2).

Cortisol concentrations were higher in Meishan sows (Figure 3a; $P < 0.01$), but no differences in postweaning cortisol day trends were detected between the two breeds. Progesterone trends after weaning were similar between the two breeds, with the exception of increased levels in White composite sows between d 12 and 15 after estrus (Figure 3b; $P < 0.01$).

Postweaning changes of FSH concentrations were different between Meishan and White composite sows (Figure 4; time \times breed interaction; $P < 0.05$). Plasma concentrations of FSH in both breeds were elevated after weaning and declined until the FSH surge (time 0; Figure 4a). Postovulatory increases in FSH declined in Meishan sows but remained elevated in White composite sows (36 to 150 h after ovulatory FSH surge). Inhibin changes after weaning were not different between Meishan and White composite sows but generally were inverse to the FSH trends (Figure 4b). Postweaning changes in LH were not different between the two breeds (data not shown). The mean values of all LH samples 24 h before the FSH surge were 2.1 ± 0.4 and 2.9 ± 0.4 ng/mL for White composite and Meishan sows,

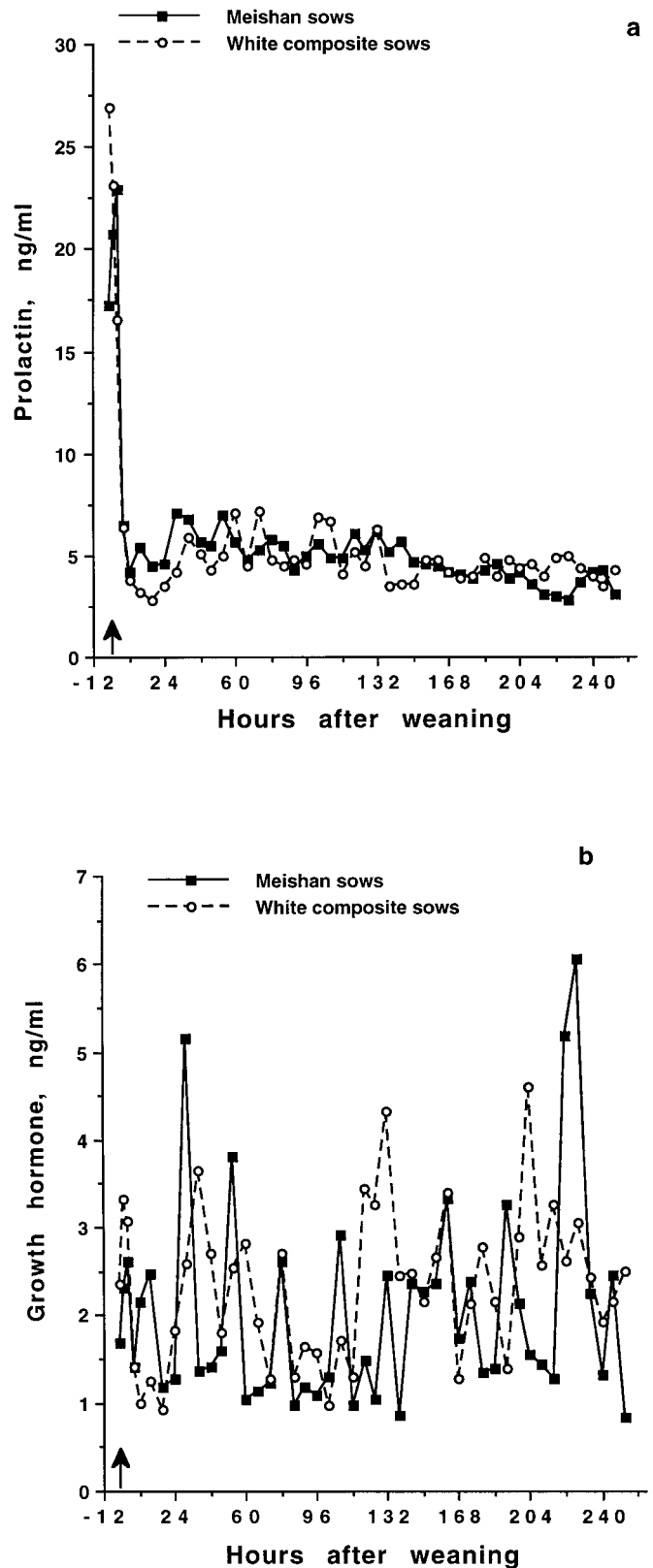


Figure 1. Changes in plasma prolactin (a) and GH (b) in White composite ($n = 6$) and Meishan ($n = 7$) sows after weaning (pigs removed at time 0 h). No breed differences were noted in changes in prolactin or GH, but prolactin significantly declined after weaning ($P < 0.01$). The SEM for prolactin was 0.76 ng/mL and GH was 0.56 ng/mL. Arrow indicates time pigs were weaned (0 h).

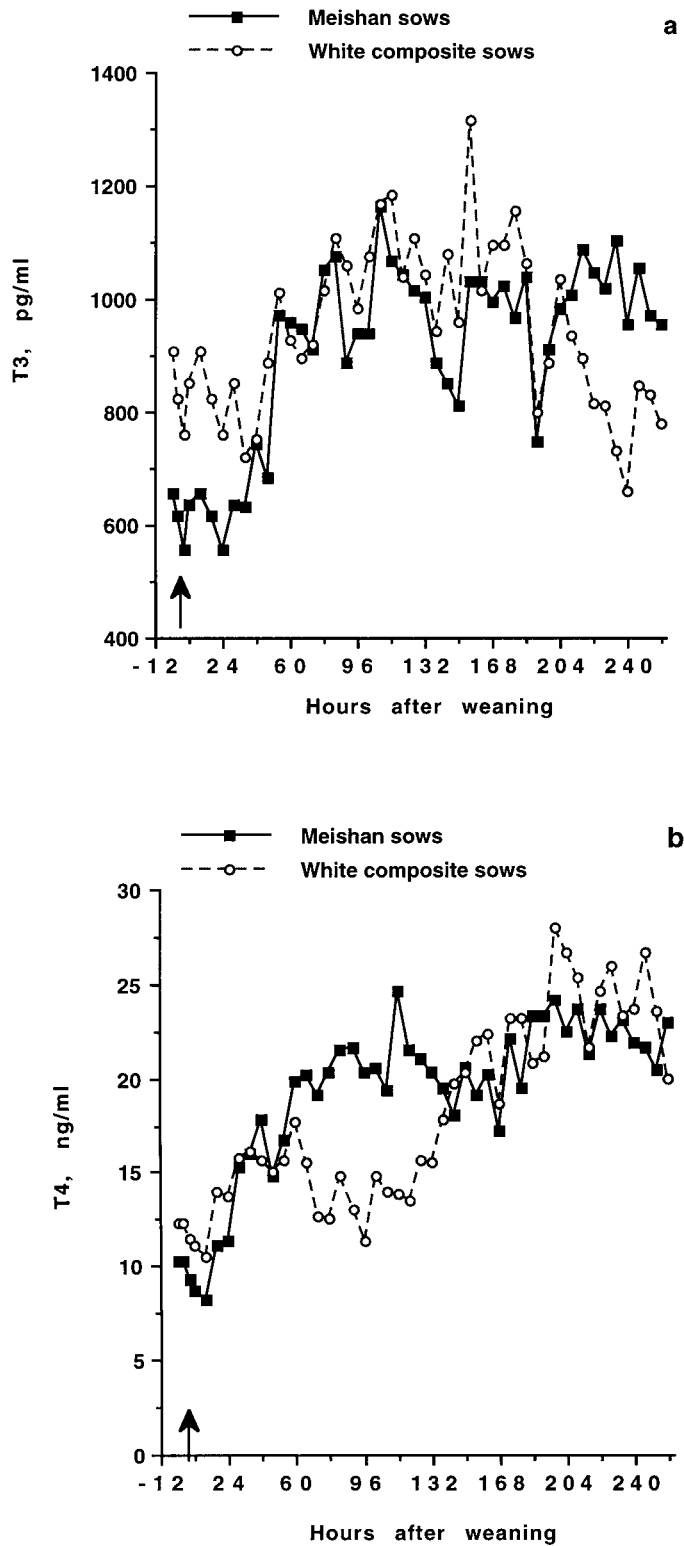


Figure 2. Changes in plasma triiodothyronine (T_3 ; a) and tetraiodothyronine (T_4 ; b) in White composite and Meishan sows after weaning. Concentrations of T_3 and T_4 after weaning in Meishan sows increased, whereas T_3 and T_4 concentrations in White composite sows were inversely related after weaning ($P < 0.05$). The SEM for T_3 was 58.8 pg/mL and for T_4 was 3.1 ng/mL. Arrow indicates time pigs were weaned (0 h).

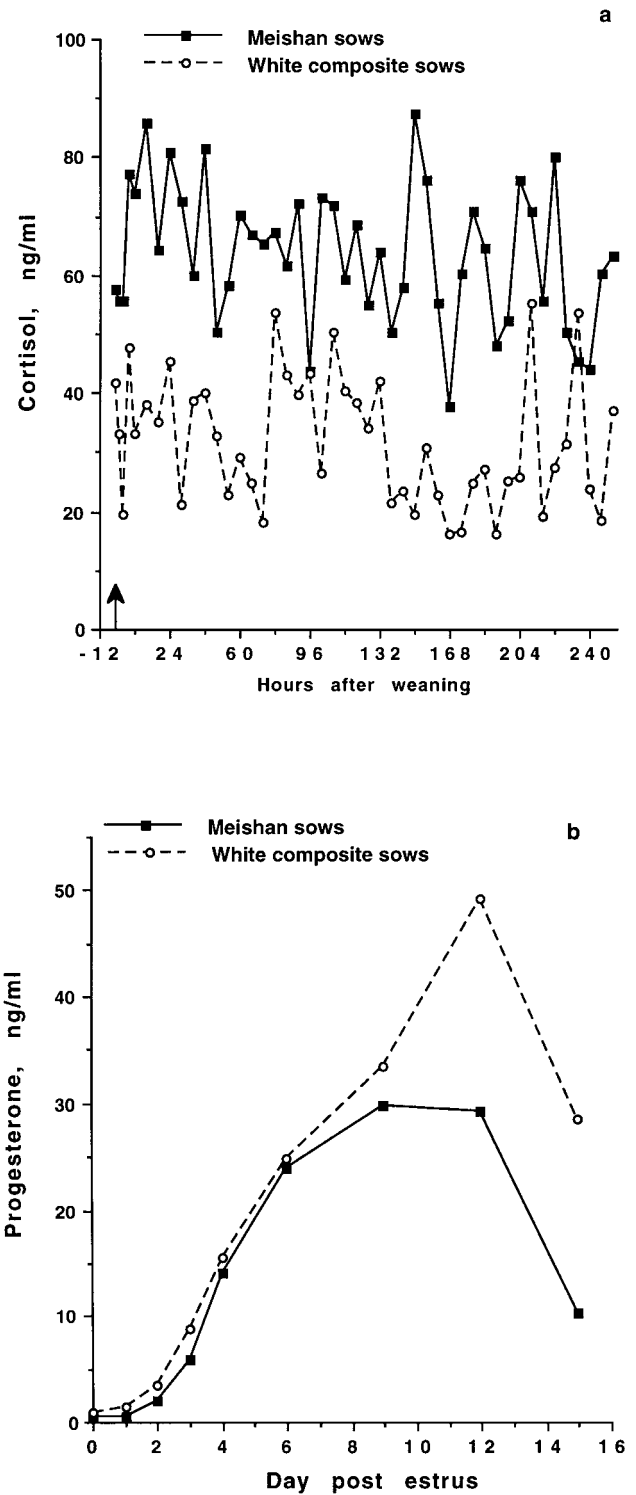


Figure 3. Changes in plasma cortisol (a) after weaning of Meishan and White composite sows. Day trends of cortisol were not different between Meishan and White composite sows, but concentrations of cortisol were increased in Meishan sows ($P < 0.01$). Arrow indicates time pigs were weaned (0 h). Panel b depicts changes in progesterone concentrations after estrus (time 0 h) in Meishan and White composite sows. Progesterone concentrations were increased in White composite sows on d 12 and 15 post estrus ($P < 0.01$). The SEM for cortisol was 6.7 ng/mL and progesterone was 2.2 ng/mL.

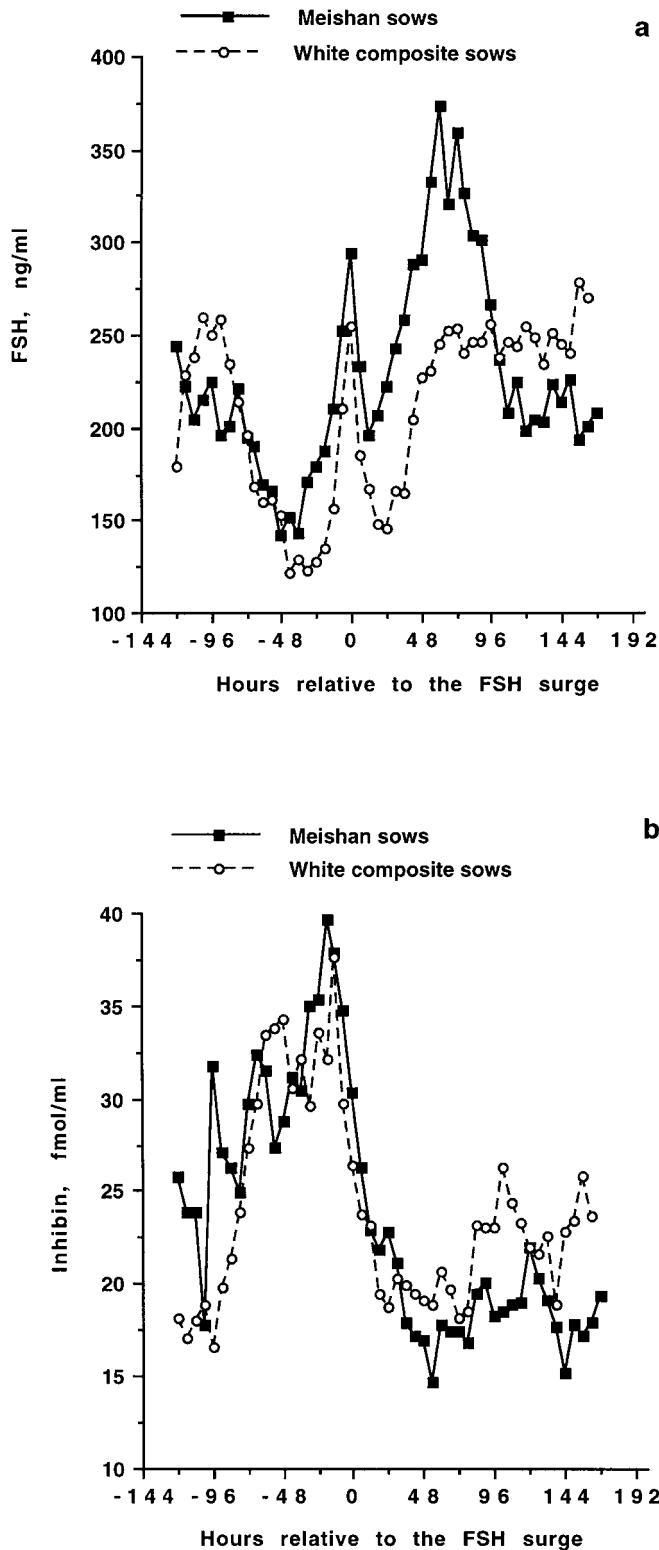


Figure 4. Changes in plasma FSH (a) and inhibin (b) in Meishan and White composite sows after weaning. All hormonal changes were adjusted to the time of the FSH surge (time 0). Profiles of FSH were different between Meishan and White composite sows in that FSH was low in Meishan sows soon after weaning and high in White composite sows ($P < 0.01$). Inhibin concentrations were not different between the two breeds. The SEM for FSH was 20.9 ng/mL and inhibin was 1.9 fmol/mL.

a respectively. The mean values of all LH samples 24 h after the FSH surge were 1.0 ± 0.5 and 1.9 ± 0.5 ng/mL for White composite and Meishan sows, respectively.

Changes in IGF-I and estradiol were synchronized to the FSH surge after weaning. Concentrations of IGF-I were similar between Meishan and White composite sows, but there was a trend for IGF-I to be higher in Meishan sows after the preovulatory FSH surge ($P < 0.10$; Figure 5a). Postweaning estradiol concentrations were increased in Meishan sows as compared with White composite sows ($P < 0.05$; Figure 5b).

Luteal Phase Endocrine Changes

At both doses of GnRH (15 and 150 ng/kg BW), White composite sows had a larger LH surge ($P < 0.05$; Figures 6 and 7) and greater plasma LH compared with Meishan females. Concentrations of FSH were greater in White composite sows than in Meishan gilts. The slope of decline of LH and FSH after peak plasma concentration was significantly more negative (i.e., a more rapid rate of disappearance) for White composite females with low-GnRH challenge (-0.0026 vs -0.0054 for LH and -0.13 vs -0.27 for FSH in Meishan vs White composite, respectively) and medium-GnRH challenge (-0.0061 vs -0.0089 for LH and -0.31 vs -0.54 for FSH in Meishans vs White composite, respectively). Progesterone concentrations were unaffected by the GnRH challenges and also were not different between breeds (Meishan = 12.3 ± 1.8 vs White composite = 10.59 ± 1.8 ng/mL). Cortisol concentrations were not affected by GnRH treatment (15 or 150 ng/kg BW), but Meishan females had significantly greater ($P < 0.01$) cortisol concentrations than White composite females (Figure 8).

After the second dose of GnRH, animals were ovariectomized. Ovulation rates were 13.6 ± 0.36 for White composite sows and 18.3 ± 0.32 and 21.2 ± 0.37 ($P < 0.01$) for young and aged Meishan females, respectively. After ovariectomy, LH concentrations of White composite sows were increased over Meishan gilts and sows ($P < 0.05$) and increased at a rate faster in White composite than Meishan females ($P < 0.05$; Figure 9a). There were no differences between White composite and Meishan females in the levels or slope of FSH increases after ovariectomy (Figure 9b). Before ECP treatment, levels of LH were increased in White composite sows compared with Meishan females ($P < 0.01$; Figure 9c). Declines in LH from ECP challenge were not different between breed groups. Pretreatment FSH levels, although elevated in White composite females (Figure 9d), were not different from Meishan females; decreases in FSH after ECP treatment were comparable in all breed groups.

To monitor possible differences in sensitivity at the pituitary level, a GnRH antagonist (Centorexil, SB-75) was administered to the ovariectomized females (9 d after ECP challenge). All doses of the GnRH antagonist gave comparable results, were not different from each other, and thus were combined for analysis. Pretreat-

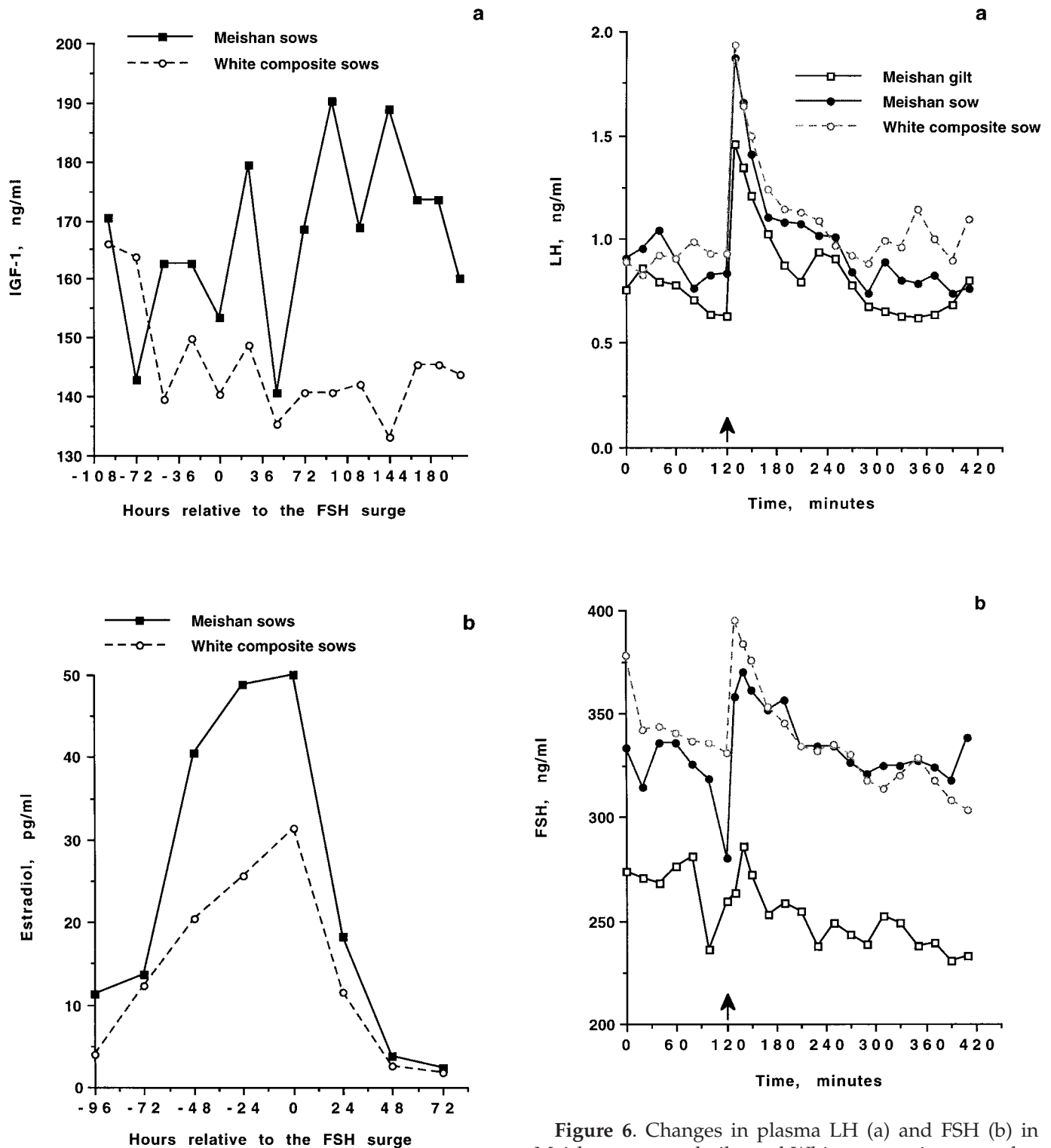


Figure 5. Changes in plasma IGF-I (a) and estradiol (b) concentrations after weaning in Meishan and White composite sows. Hormonal changes were adjusted to the time of the FSH surge (time 0 h). The IGF-I concentrations were not different during the period of follicular development (-100 h to 0 h) between the two breeds but tended to be increased in Meishan sows after the FSH surge ($P < 0.10$). Estradiol concentrations were elevated in Meishan sows ($P < 0.05$). The SEM for IGF-I was 15.9 ng/mL and estradiol was 3.0 pg/mL.

Figure 6. Changes in plasma LH (a) and FSH (b) in Meishan sows and gilts and White composite sows after GnRH challenge (15 ng/kg BW) during the luteal phase of the estrous cycle. White composite sows had a larger LH surge and increased levels of LH ($P < 0.05$). White composite sows and Meishan sows had increased FSH as compared with Meishan gilts ($P < 0.05$). The SEM for LH was 0.08 ng/mL and FSH was 11.5 ng/mL. Arrow indicates time of GnRH injection.

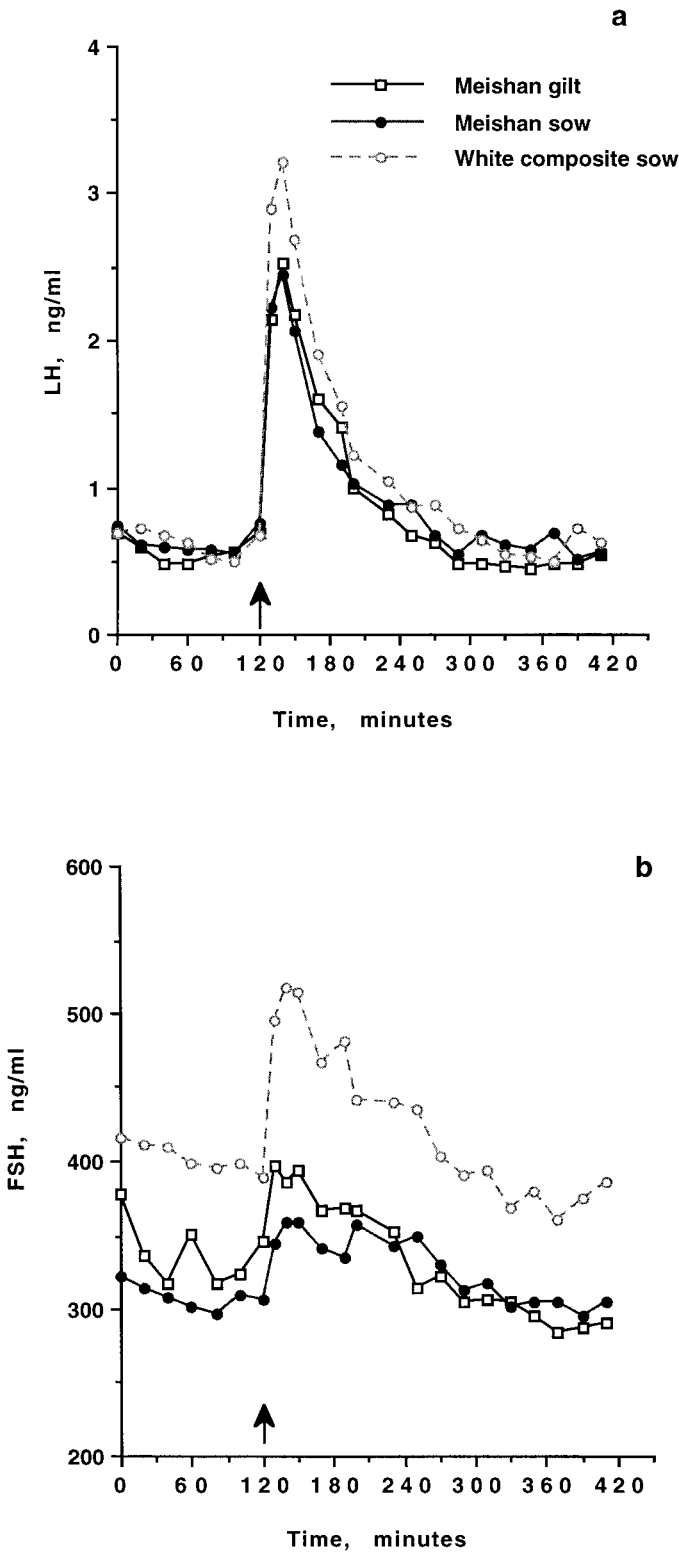


Figure 7. Changes in plasma LH (a) and FSH (b) in Meishan sows and gilts and White composite sows after GnRH challenge (150 ng/kg BW) during the luteal phase of the estrous cycle. White composite sows had a larger LH surge and increased levels of LH ($P < 0.05$). White composite sows had increased FSH as compared with Meishan gilts ($P < 0.05$). The SEM for LH was 0.13 ng/mL and FSH was 14.0 ng/mL. Arrow indicates time of GnRH injection.

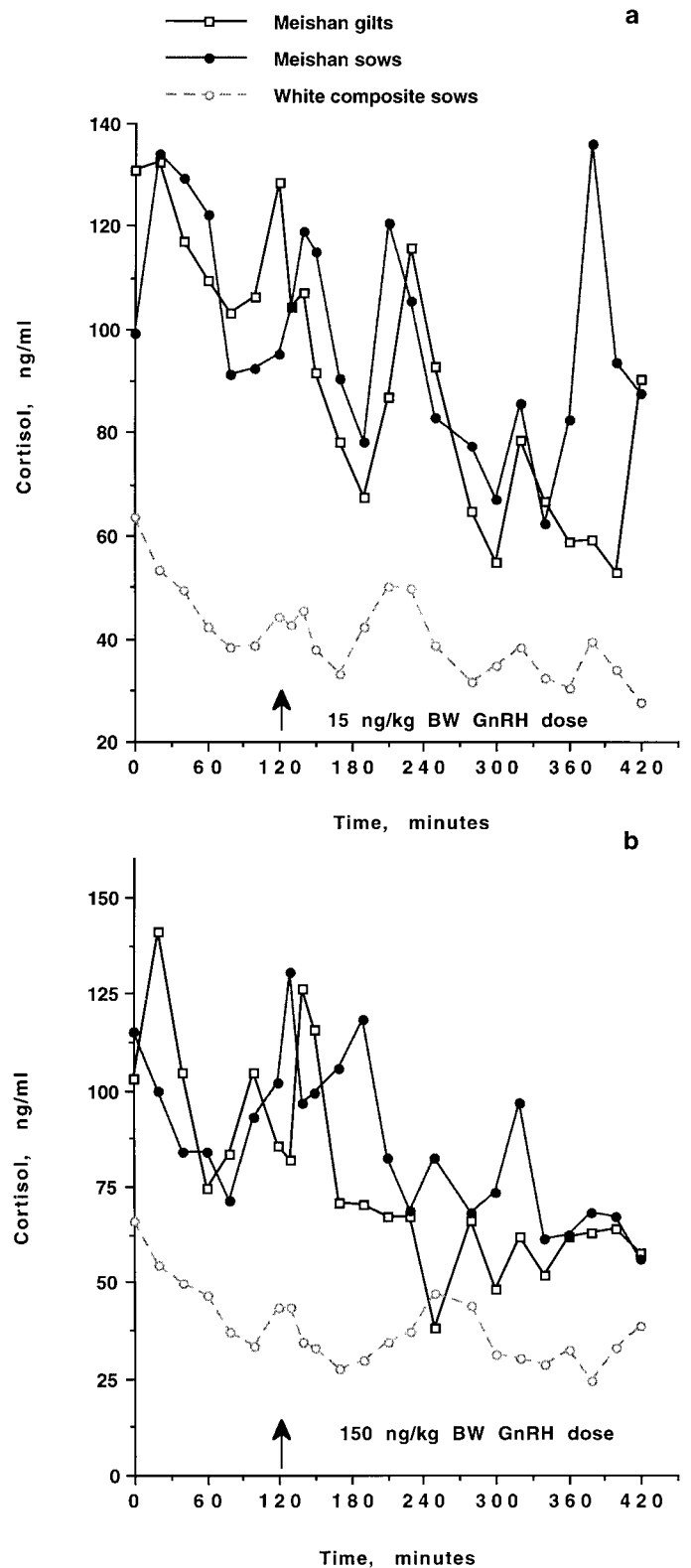


Figure 8. Changes in plasma cortisol in Meishan sows and gilts and White composite sows after a low-GnRH challenge (15 ng/kg BW; a) and high-GnRH challenge (150 ng/kg BW; b). Cortisol concentrations were not affected by GnRH, but Meishan females had significantly greater ($P < 0.01$) cortisol than White composite females. The cortisol SEM was 11.0 ng/mL. Arrow indicates time of GnRH injection.

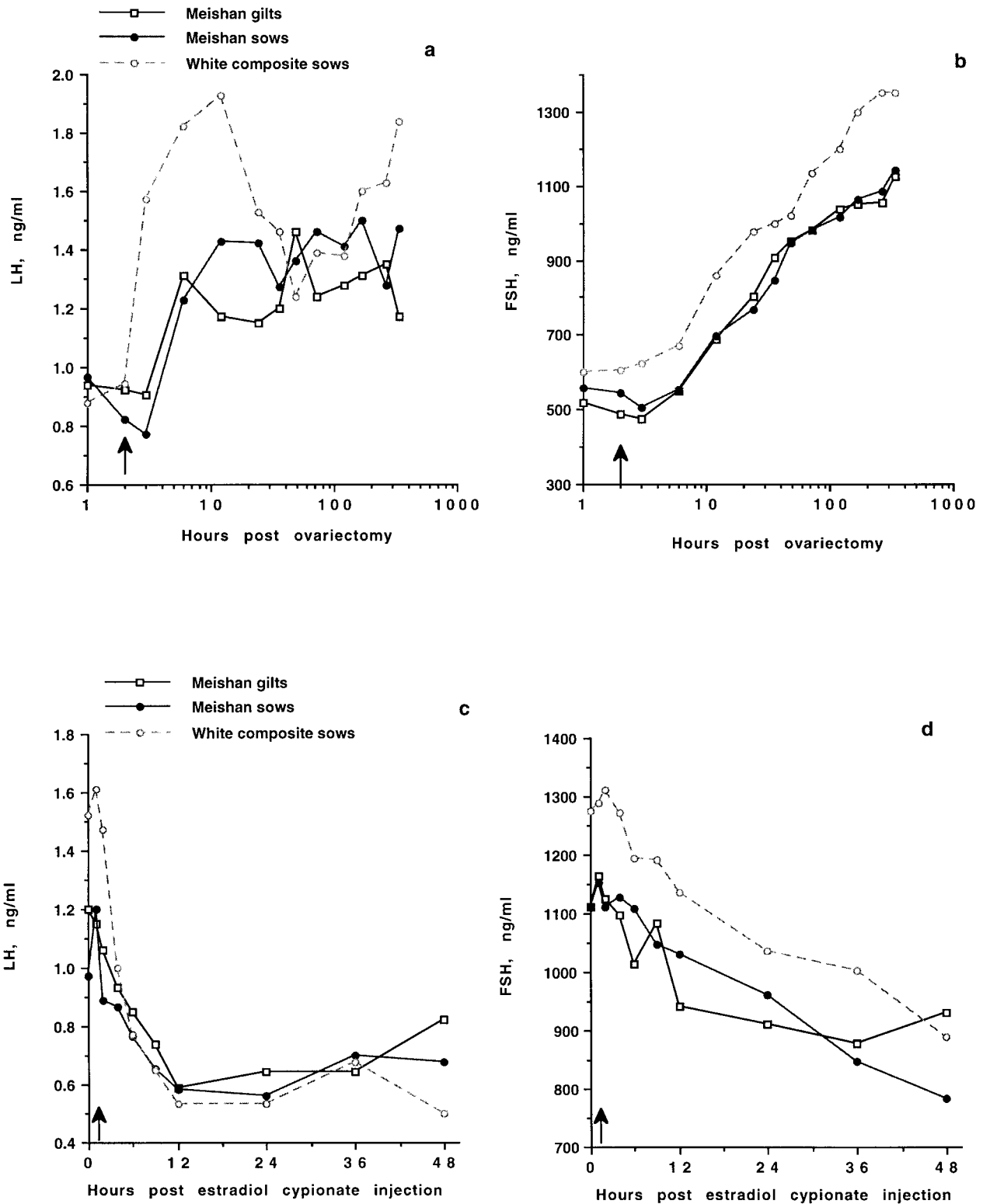


Figure 9. Changes in plasma LH (a) and FSH (b) in Meishan and White composite females after ovariectomy. Concentrations of LH increased faster in White composite females ($P < 0.05$) than Meishan females, and LH concentrations in White composite sows were elevated over those in Meishan females. There were no differences in slope of FSH increase or levels between females of Meishan and White composite breeds after ovariectomy (b). Arrow indicates time of ovariectomy. Figures c and d are LH (c) and FSH (d) changes in response to ECP challenge in ovariectomized Meishan and White composite females. Pretreatment levels of LH were elevated in White composite females ($P < 0.01$), but declines in LH were not different in breed or age groups. Declines in FSH after ECP challenge (d) was also comparable in all breed groups. The SEM for LH was 0.08 ng/mL and FSH was 40 ng/mL. Arrow indicates time of ECP injection.

ment levels of LH or FSH were not different between breeds. After GnRH antagonist depression of LH, the slope of increase of LH was greater in Meishan than in White composite females ($P < 0.01$; Figure 10a). White composite females demonstrated only a short-term response in FSH concentrations to GnRH antagonist (Figure 10b), and Meishan females demonstrated a longer decline in FSH concentrations (breed \times time interaction; $P < 0.02$).

Discussion

With the historical evidence that ovarian function (follicular recruitment, maturation, and ovulation) is endocrine-driven and primarily the response to pituitary stimulation, one might be able to establish differences in endocrine mechanisms between two breeds of swine that have different ovulation rates and litter size. After weaning of sows, ovarian function is initiated and ovulation occurs 3 to 7 d later, allowing for a time-synchronized model to compare endocrine differences in Meishan and White composite sows. Postpartum prolactin declines in the sow have been extensively studied due to the initial hypothesis that elevated prolactin levels associated with lactation would have an inhibitory effect on follicular function in sows (Stevenson et al., 1981; Kirkwood et al., 1984; Foxcroft et al., 1987). Prolactin changes in this study were similar for Meishan and White composite sows even though Meishan sows came into estrus sooner than White composite sows. Effects of removal of piglets from the sow and subsequent weaning can easily be seen in the precipitous decline in prolactin concentrations, but no differences in prolactin changes were detected between Meishan and White composite sows. In contrast to the greater plasma FSH, LH, and testosterone concentrations found in Meishan than in White composite boars (Wise et al., 1996, 2000), there are few endocrine differences noted between Meishan and White composite (or White European breeds) females during the estrous period (Hunter et al., 1993). Some studies report increased estrogen and inhibin production associated with the increased number of follicles in Meishan females but few gonadotropic differences have been associated with this increase in follicles (Hunter et al., 1996).

Few major differences in reproductive hormones after weaning between Meishan and White composite sows were noted in this study even though the breeds are quite dissimilar. As Chinese Meishan pigs are considerably different in size, fat content, muscling, and general physical characteristics than White composites of European origin, differences in metabolic hormones may be evident that influence reproductive responses. Metabolic hormones (T_3 , T_4 , GH, IGF-I) may also undergo major changes during lactation and after weaning. Concentrations of T_3 and T_4 were monitored in sows after weaning because thyroid-stimulating hormone concentrations are increased in Meishan boars and sows as

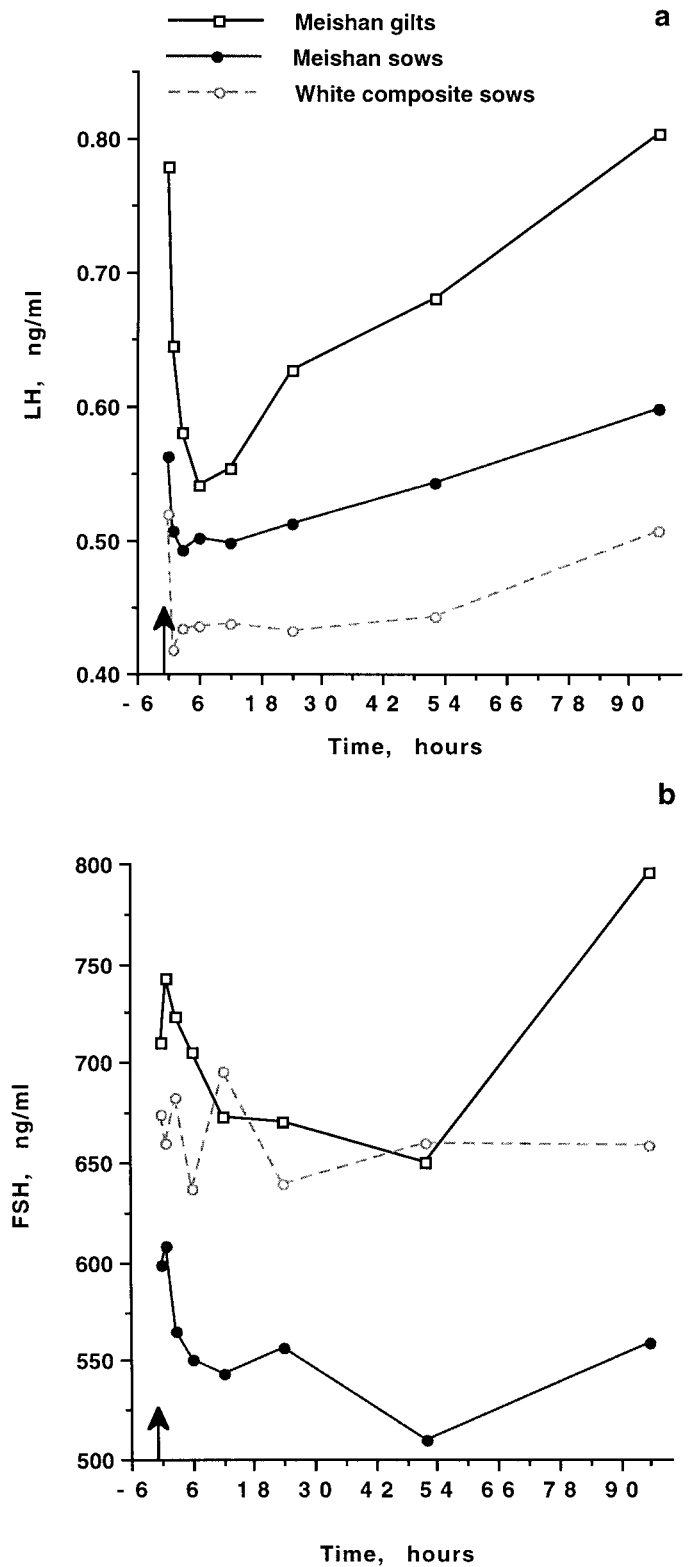


Figure 10. Changes in plasma LH (a) and FSH (b) in ovariectomized Meishan sows and gilts and White composite sows after GnRH antagonist (responses to 2, 10, or 50 $\mu\text{g}/\text{kg}$ BW of GnRH antagonist were not different and thus were combined for analysis and presentation). The SEM for LH was 0.06 and FSH was 21.0 ng/mL. Arrow indicates time of GnRH antagonist injection.

compared with White composites (Li et al., 1996). Surprisingly, concentrations of T_3 and T_4 were not different between Meishan and White composite sows, but postweaning temporal changes of T_3 and T_4 were different between breeds. Shortly after weaning, there were differences in FSH trends between Meishan and White composite sows. Increased levels of inhibin in Meishan sows noted by Hunter et al. (1993, 1996; follicular phase) were not detected in this study. Postweaning changes of inhibin concentrations indicate an inverse relationship with FSH (Hasegawa et al., 1988) and support the quick increase in inhibin concentrations after weaning noted by Trout et al. (1992).

As reported in other studies (Hunter et al., 1996), estradiol concentrations were elevated in Meishan sows and probably reflected the increased numbers of developing follicles. Follicular fluid and granulosa production of estradiol *in vitro* are greater in Meishan as compared with Large White hybrids (Miller et al., 1998). Greater FSH secretion concurrent with increased estradiol concentrations in Meishan sows supports less-sensitive negative feedback on gonadotropin release (Tilton et al., 1994). Secretion of FSH in castrated Meishan males increases faster after depression with exogenous testosterone and estradiol than observed in White composite castrates (Wise et al., 1996). Differences in the trends of FSH and T_3 after weaning between the breeds may have biological meaning or relate to the shorter time to estrus after weaning in Meishan sows.

Changes and concentrations of cortisol after weaning were similar to those noted by Ash and Heap (1975) in Large White sows. The only hormone exhibiting a major concentration difference between breeds was cortisol, which was elevated in Meishan females both after weaning and during the estrual period. Hay and Mormede (1998) have reported that urinary corticoids were fivefold higher in Meishan than Large White sows, and Farmer et al. (2000) observed greater cortisol concentrations during late pregnancy in Meishan sows. Meishan males also have elevated cortisol compared with White composite boars (Wise et al., 2000).

Turner et al. (1998) noted that presumed stress that doubled cortisol levels in gilts did not alter ovulation rate, pregnancy, or numbers of embryos as compared with controls; thus, the relationship of increased cortisol concentrations associated with stress and declines of reproductive efficiency may have to be reevaluated in swine. Stress or body responses to increased cortisol concentrations differ among individuals; thus, some animals are truly under duress and decline in productive functions, whereas others thrive (Turner et al., 1999). Acute increases in cortisol do not alter the LH surge, estrus, or ovulation in swine, but sustained increases of cortisol will inhibit reproduction (Turner et al., 1999). In contrast, sustained increases of cortisol found in Meishan females did not negatively affect reproduction and may have had a positive effect at the ovarian level. Increased corticoids found in Meishan females could increase cholesterol in granulosa cells for increased sub-

strate for steroid synthesis (Townes et al., 1999). Cortisol can augment the LH response in granulosa cells *in vitro* (Keren-Tal et al., 1993) and increase pituitary content of FSH, FSH β -subunit mRNA, and serum FSH bioactivity (McAndrews et al., 1994; Kilen et al., 1996). The mechanism of increased cortisol concentrations in the Meishan breed is unknown. Concentrations of ACTH in Meishan pigs do not seem to be elevated over White breeds (Klemcke and Christenson, 1997; Desautels et al., 1999), and adrenal weights are not increased in Meishan pigs (unpublished observations).

In the second experiment after GnRH treatment, slopes of decline of LH and FSH in White composite females were greater than in Meishans. After GnRH antagonist, the slope of increase of LH was also greater in Meishan females, which could be related to a slower clearance. Increased levels of gonadotropins found in White composite females as compared with Meishans in this study and others (Tilton et al., 1994) may not be a biologically relevant comparison if gonadotropins in White breeds are cleared at different rates or have differential binding to receptors. In ovariectomized Meishan and Large White gilts, GnRH challenge resulted in increased circulating LH and FSH in the Large White, and these hormones remained elevated longer (Tilton et al., 1994). Consistent differences between Meishan and White composite males (Wise et al., 2000) and females may be related to the period of time that gonadotropins are in peripheral circulation. Although it is known that there are no differences in the number of glycosylation sites in the α - and β -subunits of FSH or LH (Li and Ford, 1998; Li et al., 2000) in Meishan and White composite females, there may be differences in the sugar and sulfate moieties that influence clearance and receptor binding (Bousfield et al., 1996; Zerfaoui and Ronin, 1996; Lambert et al., 1998).

A major genetic effect on ovulation rate has been mapped to chromosome 8 of the pig (Rohrer et al., 1999); mapping analysis indicated that both White composite and Meishan alleles contribute to increase ovulation rate. In support of the endocrine data in these studies (that indicate few reproductive endocrine differences between Meishan and White composite females), reproductive hormones (i.e., FSH, LH, or inhibin) or their receptors do not map to the chromosomal locations affecting ovulation rate (chromosome 8).

Implications

The economic advantage of increased ovulation rates and litter size found in the Meishan breed would be useful to swine breeders and producers if these traits could be transferred to other breeds. The mechanisms of action and genes responsible for this increased reproductive efficiency require identification to accomplish this transfer. With the exception of cortisol, there are not large differences in circulating hormone concentrations between Meishan and White composite females that would help to easily identify the mechanism of

increased ovarian function found in Meishan females. Elevated cortisol concentrations have been historically associated with stress and declines of reproductive efficiency, but these relationships may have to be reevaluated in light of the increases in reproductive efficiency of the Meishan breed and surprisingly high circulating cortisol concentrations.

Literature Cited

- Adashi, E. Y., P. B. C. Jones, and A. J. W. Hsueh. 1981. Synergistic effect of glucocorticoids on the stimulation of progesterone production by follicle-stimulating hormone in cultured rat granulosa cells. *Endocrinology* 109:1888–1894.
- Ash, R. W., and R. B. Heap. 1975. Oestrogen, progesterone and corticosteroid concentrations in peripheral plasma of sows during pregnancy, parturition, lactation and after weaning. *J. Endocrinol.* 64:141–154.
- Barkan, D., H. Jia, A. Dantes, L. Vardimon, A. Amsterdam, and M. Rubinstein. 1999. Leptin modulates the glucocorticoid-induced ovarian steroidogenesis. *Endocrinology* 140:1731–1738.
- Bousfield, G. R., V. Y. Butnev, R. R. Gotschall, V. L. Baker, and W. T. Moore. 1996. Structural features of mammalian gonadotropins. *Mol. Cell. Endocrinol.* 125:3–19.
- Christenson, R. K. 1993. Ovulation rate and embryonic survival in Chinese Meishan and white crossbred pigs. *J. Anim. Sci.* 71:3060–3066.
- Desautels, C., A. Sarrieu, J. C. Caritez, and P. Mormede. 1999. Behavior and pituitary-adrenal function in large white and Meishan pigs. *Domest. Anim. Endocrinol.* 16:193–205.
- Farmer, C., M. F. Palin, and M. T. Sorensen. 2000. Mammary gland development and hormone levels in pregnant Upton-Meishan and large white gilts. *Domest. Anim. Endocrinol.* 18:241–251.
- FASS. 1999. Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching. 1st rev. ed. Federation of Animal Science Societies, Savoy, IL.
- Ford, J. J. 1983. Serum estrogen concentrations during postnatal development in male pigs. *Proc. Soc. Exp. Med. Biol.* 174:160–164.
- Ford, J. J., T. H. Wise, and D. D. Lunstra. 1997. Negative relationship between blood concentrations of follicle-stimulating hormone and testicular size in mature boars. *J. Anim. Sci.* 75:790–795.
- Foxcroft, G. R., H. J. Shaw, M. G. Hunter, P. J. Booth, and R. T. Lancaster. 1987. Relationships between luteinizing hormone, follicle-stimulating hormone and prolactin secretion and ovarian follicular development in the weaned sow. *Biol. Reprod.* 36:175–191.
- Hasegawa, Y., K. Miyamoto, S. Iwamura, and M. Igarashi. 1988. Changes in serum concentrations of inhibin in cyclic pigs. *J. Endocrinol.* 118:211–219.
- Hay, M., and P. Mormede. 1998. Urinary excretion of catecholamines, cortisol and their metabolites in Meishan and large white sows: validation as a non-invasive and integrative assessment of adrenocortical and sympathoadrenal axis activity. *Vet. Res. (Paris)* 29:119–128.
- Houseknecht, K. L., D. L. Boggs, D. R. Champion, J. L. Sartin, T. E. Kiser, G. B. Rampacek, and H. E. Amos. 1988. Effect of dietary energy source and level on serum growth hormone, insulin-like growth factor 1, growth and body composition in beef heifers. *J. Anim. Sci.* 66:2916–2923.
- Howard, H. J., and J. J. Ford. 1992. Relationships among concentrations of steroids, inhibin, insulin-like growth factor-1 (IGF-1), and IGF-binding proteins during follicular development in weaned sows. *Biol. Reprod.* 47:193–201.
- Hunter, M. G., C. Biggs, G. R. Foxcroft, A. S. McNeilly, and J. E. Tilton. 1993. Comparisons of endocrinology and behavioural events during the periovulatory period in Meishan and large-white hybrid gilts. *J. Reprod. Fertil.* 97:475–480.
- Hunter, M. G., C. Biggs, A. R. Pickard, and L. S. Faillace. 1994. Differences in follicular aromatase activity between Meishan and large-white hybrid gilts. *J. Reprod. Fertil.* 101:139–144.
- Hunter, M. G., H. M. Picton, C. Biggs, G. E. Mann, A. S. McNeilly, and G. R. Foxcroft. 1996. Periovulatory endocrinology in high ovulating Meishan sows. *J. Endocrinol.* 150:141–147.
- Keren-Tal, I., A. Dantes, R. Sprengel, and A. Amsterdam. 1993. Establishment of steroidogenic granulosa cell lines expressing follicle stimulating hormone receptors. *Mol. Cell. Endocrinol.* 95:R1–R10.
- Kilen, S. M., M. Szabo, G. A. Strasser, J. M. McAndrews, S. J. Ringstrom, and N. B. Schwartz. 1996. Corticosterone selectively increases follicle-stimulating hormone beta-subunit messenger ribonucleic acid in primary anterior pituitary cell culture without affecting its half-life. *Endocrinology* 137:3802–3807.
- Kirkwood, R. N., K. R. Lapwood, W. C. Smith, and I. L. Anderson. 1984. Plasma concentrations of LH, prolactin, oestradiol-17 β and progesterone in sows weaned after lactation for 10 or 35 days. *J. Reprod. Fertil.* 70:95–102.
- Klemcke, H. G., and R. K. Christenson. 1997. Porcine fetal and maternal adrenocorticotrophic hormone and corticosteroid concentrations during gestation and their relation to fetal size. *Biol. Reprod.* 57:99–106.
- Klindt, J., J. J. Ford, J. G. Berardinelli, and L. L. Anderson. 1983. Growth hormone secretion after hypophysial stalk transection in pigs. *Proc. Soc. Exp. Biol. Med.* 172:508–513.
- Klindt, J., and R. T. Stone. 1984. Porcine growth hormone and prolactin: concentrations in the fetus and secretory patterns in the growing pig. *Growth* 48:1–15.
- Lambert, A., J. A. Talbot, C. J. Anobile, and W. R. Robertson. 1998. Gonadotrophin heterogeneity and biopotency: implications for assisted reproduction. *Molec. Human Reprod.* 4:619–629.
- Li, M. D., and J. J. Ford. 1998. A comprehensive evolutionary analysis based on nucleotide and amino acid sequences of the α - and β -subunits of glycoprotein hormone gene family. *J. Endocrinol.* 156:529–542.
- Li, M. D., R. L. Matteri, G. J. Macdonald, T. H. Wise, and J. J. Ford. 1996. Overexpression of β -subunit of thyroid-stimulating hormone in Meishan swine identified by differential display. *J. Anim. Sci.* 74:2104–2111.
- Li, M. D., G. S. Rohrer, T. H. Wise, and J. J. Ford. 2000. Identification and characterization of a new allele for the beta subunit of follicle-stimulating hormone in Chinese pig breeds. *Anim. Genet.* 31:28–30.
- McAndrews, J. M., S. J. Ringstrom, K. D. Dahl, and N. B. Schwartz. 1994. Corticosterone *in vivo* increases pituitary follicle-stimulating hormone (FSH)- β messenger ribonucleic acid content and serum FSH bioactivity selectively in female rats. *Endocrinology* 134:158–163.
- Miller, A. T., H. M. Picton, J. Craigon, and M. G. Hunter. 1998. Follicle dynamics and aromatase activity in high-ovulating Meishan sows and in Large-White hybrid contemporaries. *Biol. Reprod.* 58:1372–1378.
- Rohrer, G. A., J. J. Ford, T. H. Wise, J. L. Vallet, and R. K. Christenson. 1999. Identification of quantitative trait loci affecting female reproductive traits in a multigeneration Meishan-White composite swine population. *J. Anim. Sci.* 77:1385–1391.
- Schanbacher, B. 1988. Radioimmunoassay of inhibin: Serum responses to unilateral and bilateral orchidectomy. *Endocrinology* 123:2323–2330.
- Snedecor, G. W., and W. G. Cochran. 1974. *Statistical Methods*. 6th ed. p 84. Iowa State University Press, Ames.
- Spicer, L. J., and C. S. Chamberlain. 1998. Influence of cortisol on insulin- and insulin-like growth factor 1 (IGF-1)-induced steroid production and on IGF-1 receptors in cultured bovine granulosa cells and thecal cells. *Endocrine* 9:153–161.
- Stevenson, J. S., N. M. Cox, and J. H. Britt. 1981. Role of the ovary in controlling luteinizing hormone, follicle stimulating hormone, and prolactin secretion during and after lactation in pigs. *Biol. Reprod.* 24:341–353.

- Tetsuka, M., M. Milne, G. E. Simpson, and S. G. Hillier. 1999. Expression of 11β -hydroxysteroid dehydrogenase, glucocorticoid receptor, and mineralocorticoid receptor genes in rat ovary. *Biol. Reprod.* 60:330–335.
- Tilton, J. E., C. Biggs, M. G. Hunter, and G. R. Foxcroft. 1994. Gonadotropin secretion in ovariectomized Chinese Meishan and hybrid Large White gilts; responses to challenges with estradiol benzoate, gonadotropin-releasing hormone, or porcine follicular fluid. *Biol. Reprod.* 51:963–970.
- Towns, R., K. M. J. Menon, R. K. Brabec, A. M. Silverstein, J. M. Cohen, J. M. Bowen, and P. L. Keyes. 1999. Glucocorticoids stimulate the accumulation of lipids in the rat corpus luteum. *Biol. Reprod.* 61:416–421.
- Trout, W. E., J. H. Killen, R. K. Christenson, B. D. Schanbacher, and J. J. Ford. 1992. Effects of weaning on concentrations of inhibin in follicular fluid and plasma of sows. *J. Reprod. Fertil.* 94:107–114.
- Turner, A. I., P. H. Hemsworth, B. J. Canny, and A. J. Tilbrook. 1999. Sustained but not repeated acute elevation of cortisol impaired the luteinizing hormone surge, estrus, and ovulation in gilts. *Biol. Reprod.* 61:614–620.
- Turner, A. I., P. H. Hemsworth, P. E. Hughes, and A. J. Tilbrook. 1998. Repeated acute activation of the hypothalamo-pituitary adrenal axis prior to and during estrus did not affect reproductive performance in gilts. *Biol. Reprod.* 58:1458–1462.
- Wise, T., J. Klindt, J. J. Ford, and R. K. Christenson. 1991. Changes in thymosin β_4 and gonadal function during puberty in boars and gilts immunized against estrone. *Anim. Reprod. Sci.* 24:139–152.
- Wise, T., D. D. Lunstra, and J. J. Ford. 1996. Differential pituitary and gonadal function of Chinese Meishan and European white composite boars: Effects of gonadotropin-releasing hormone stimulation, castration, and steroidal feedback. *Biol. Reprod.* 54:146–153.
- Wise, T., E. L. Zanella, D. D. Lunstra, and J. J. Ford. 2000. Relationships of gonadotropins, testosterone, and cortisol in response to GnRH and GnRH antagonist in boars selected for high and low follicle-stimulating hormone levels. *J. Anim. Sci.* 78:1577–1590.
- Zanella, E. L., D. D. Lunstra, T. H. Wise, J. E. Kinder, and J. J. Ford. 2000. GnRH antagonist inhibition of gonadotropin and steroid secretion in boars in vivo and steroid production in vitro. *J. Anim. Sci.* 78:1591–1597.
- Zerfaoui, M., and C. Ronin. 1996. Glycosylation is the structural basis for changes in polymorphism and immunoreactivity of pituitary glycoprotein hormones. *Eur. J. Clin. Chem. Clin. Biochem.* 34:749–753.

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