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RELATIONSHIPS AMONG MEASURES OF TESTICULAR DEVELOPMENT AND ENDOCRINE FUNCTION IN BOARS¹

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Summary

Nine blood samples were taken at 30-min intervals from 36 Landrace × Large White boars at each of eight ages (42, 56, 70, 84, 98, 112, 126 and 140 d). Serum concentrations of luteinizing hormone (LH), follicle-stimulating hormone (FSH), testosterone (T) and estradiol-17β (E₂) were quantified by radioimmunoassay procedures. The maximum concentration of LH and the age at maximum concentration were predicted for each boar. Variability of LH samples was described for each boar by the pooled within age variance among LH samples and by the number of LH peaks. Measurements of testicular development taken at 140 d of age included: in situ testis width and length, excised testis weights and histological traits of excised testes (seminiferous tubule diameter, percentage of tubules with a lumen and percentage of tubules with active spermatogenesis). Pooled within line correlations were calculated with data from boars selected for either high or low testis weight. Correlations among the testicular traits ranged from .45 to .88. Luteinizing hormone concentration (mean over all ages) was related to measures of testicular development ($r = .24$ to $.49$). Concentrations of LH from 42 to 84 d of age were more highly correlated with testicular traits than were the concentrations from 98 to 140 d. Boars with larger, more mature testes tended to have higher maximum concentrations of LH ($r = .19$ to $.42$) and younger age at maximum concentration ($r = -.12$ to $-.26$). Testicular traits were correlated with the number of LH peaks (r

$= .31$ to $.43$) but not with LH sample variance ($r = -.14$ to $-.01$). Concentration of FSH was not related ($r = -.20$ to $.19$) to measures of testicular development. Testicular traits were more highly correlated with E₂ concentration ($r = .22$ to $.41$) than with T concentration ($r = .12$ to $.33$). Correlations between gonadotropin and steroid concentrations were small and nonsignificant.

(Key Words: Swine, Testis Size, Luteinizing Hormone, Follicle-Stimulating Hormone, Testosterone, Estradiol-17β.)

Introduction

Reproductive traits affect efficiency of swine production. However, selection has not been widely practiced for reproductive traits because they have low heritabilities. A moderately heritable trait, measurable on males and related to female reproduction would be useful in selection for increased female reproductive performance.

Gonads of both sexes have similar hormonal control systems (Land and Carr, 1979). Testicular development, spermatogenesis and steroid production in the male are controlled by follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which have parallel roles in controlling ovarian function. Evidence suggests that the same autosomal genes control these hormones in both sexes. Male and female mice from a line selected for high induced ovulation rate had increased gonadal sensitivity to FSH (Wolfe et al., 1981). Ewes and rams of the Finnish Landrace breed were less sensitive to negative feedback of steroids and had earlier pubertal releases of LH than did those of other, less prolific breeds (Land and Lee, 1976).

Selection for testis size, possibly in combination with measures of reproductive hormone concentrations, may alter endocrine systems such that reproductive performance will be

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improved. The objective of this study was to estimate the relationships between measures of testicular growth and reproductive hormone concentrations in boars.

Materials and Methods

Thirty-six Landrace \times Large White cross boars were selected from litters with either high or low predicted genetic merit for 150-d paired testis weight. Details of selection of 16 boars with low testis weight (LTW) and 20 boars with high testis weight (HTW), boar management, data collection and data analyses were previously described (Schinckel et al., 1984). Determination of luteinizing hormone (LH), follicle-stimulating hormone (FSH), testosterone (T) and estradiol-17 β (E₂) concentrations were made at eight ages (42, 56, 70, 84, 98, 112, 126 and 140 d). At 140 d of age, in situ testis width and length measurements were taken, boars were probed for backfat thickness, castrated and testis and epididymis weights were determined. Testicular tissue samples were fixed for 24 h in Bouins fluid and then transferred to 70% ethanol. Fixed tissues were embedded in paraffin wax and 5- μ m sections were stained with hematoxylin-eosin. Mean seminiferous tubule diameter was calculated from the measurement of 40 round tubules/boar. The percentage of tubules with a lumen and with active spermatogenesis (presence of spermatids) was estimated from the evaluation of 100 tubules/boar.

Nine blood samples were taken at 30-min intervals via jugular venipuncture at each age. A composite sample for each boar was made from the samples collected each day. Serum hormone concentrations were quantified by radioimmunoassay procedures. Luteinizing hormone concentrations were determined for individual samples and T, E₂ and FSH concentrations were determined on the pooled samples.

The maximum LH concentration and age at maximum concentration were predicted for each boar by periodic regression equations and were treated as new statistics. Variability of the LH samples was described for each boar by the pooled within age sample variance and by the number of peaks between 42 and 140 d. A peak was defined as a sample whose lower 66% confidence limit was higher than the upper 66% confidence limits for the preceding and subsequent samples.

Correlations among variables were estimated from the residual variances and covariances

obtained from least-squares analysis. The model included the fixed effects of line, farrowing group and line \times farrowing group. Data analyzed included testicular measurements, body weight and backfat thickness taken at 140 d of age and hormone concentrations from 42 to 140 d. Four sets of correlations were calculated: (1) among measures of testicular development, (2) among concentrations of gonadotropins, (3) between measures of testicular development and concentrations of gonadotropins and (4) between concentrations of steroids with measures of testicular development and with concentrations of gonadotropins.

Results

Correlations among testicular traits and of testicular traits with backfat thickness and 140-d body weight are presented in table 1. Correlations among the testicular traits ranged from .45 to .88. Correlations of backfat thickness with testicular traits were between .08 and .21. Body weight was significantly correlated with epididymis weight and testis length ($r = .50$ and $.35$, respectively).

Correlations among concentrations of gonadotropins are presented in table 2. The mean and maximum predicted LH concentrations were significantly correlated ($r = .74$). The remaining correlations among the levels of gonadotropins ranged from $-.15$ to $.27$.

Correlations between testicular traits and concentrations of gonadotropins are shown in table 3. Correlations between the mean concentration of LH and testicular traits ranged from .24 to .49. Testicular development was more highly correlated with LH concentrations from 42 to 84 d of age than with LH concentrations from 98 to 140 d. Correlations between maximum predicted LH concentrations and testis traits were between .19 and .42. Correlations of age at maximum predicted LH concentration with testicular traits ranged from $-.12$ to $-.26$. Testicular traits were correlated with the number of peaks ($r = .31$ to $.43$) but not with the LH sample variance ($r = -.14$ to $-.01$). Correlations between the mean concentration of FSH and testicular traits ranged from $-.20$ to $.19$.

The correlations of testicular traits and concentrations of gonadotropins with mean concentrations of steroids are presented in table 4. Correlations of E₂ concentrations with testicular traits ranged from .22 to .41. Correlations of T concentrations with testicular traits were between .12 and .33. The correlations

TABLE 1. CORRELATIONS AMONG TESTICULAR TRAITS AND OF TESTICULAR TRAITS WITH BODY WEIGHT AND BACKFAT THICKNESS^a

Item	Testis weight	Epididymis weight (1)	Testis width (2)	Testis length (3)	Percentage sperm ^b (4)	Percentage lumen ^b (5)	Tubule diameter ^b
Testis weight (1)		.65**	.88**	.88**	.76**	.72**	.80**
(2)			.63**	.67**	.53**	.45**	.59**
(3)				.71**	.71**	.88**	.90**
(4)					.68**	.66**	.86**
(5)						.94**	.80**
Backfat thickness	.08	.21	.10	.08	.20	.21	.14
Body weight	.13	.50**	.24	.35*	-.12	-.08	.12

^aCorrelations pooled within line and farrowing group (36 boars).

^bPercentage sperm = percentage of seminiferous tubules with active spermatogenesis. Percentage lumen = percentage of seminiferous tubules with a lumen. Tubule diameter = seminiferous tubule diameter.

*P<.05.

**P<.01.

between levels of gonadotropins and steroids were small and nonsignificant.

Correlations between LH concentrations from adjacent age periods ranged from -.05 to .48. Correlations between concentrations of FSH from adjacent ages from 42 to 84 d of age ranged from .27 to .80 and those from 98 to 140 d were between .43 and .84. No relationship was found between FSH concentrations at 84 and 98 d of age, the time period during which FSH concentration rapidly increased. Correlations between concentrations of T from adjacent age periods ranged from .07 to .70. A positive relationship was also found between

concentrations of E₂ from adjacent sampling ages ($r = .09$ to $.57$). The remaining correlations among concentrations of hormones at the same or at different ages were very small.

Discussion

The significant correlations between measures of testis size and percentage of tubules with active spermatogenesis suggest that boars with large testes are sexually more mature at 140 d of age and are producing greater numbers of sperm cells. Schinckel et al. (1983) reported correlations of approximately .56 between similar measures of testis size and percentage of

TABLE 2. CORRELATIONS AMONG CONCENTRATIONS OF GONADOTROPINS^a

Item	LH	(1)	(2)	(3)	(4)
Maximum predicted LH concentration (1)		.74**			
Age at maximum predicted LH concentration (2)		-.10	-.16		
Variance of the LH samples (3)		.27 [†]	.14	.08	
No. of peaks (4)		.25	.15	-.08	-.13
FSH		.03	.15	-.09	-.15
					-.09

^aCorrelations pooled within line and farrowing group (36 boars). LH = mean concentration of luteinizing hormone from 42 to 140 d of age; no. of peaks = number of LH peaks observed from 42 to 140 d of age; FSH = mean concentration of follicle-stimulating hormone from 42 to 140 d of age.

[†]P<.10.

**P<.01.

TABLE 3. CORRELATIONS BETWEEN TESTICULAR TRAITS AND CONCENTRATIONS OF GONADOTROPINS^a

Gonadotropin measurement ^b	Testicular traits ^c						
	Testis weight	Epididymis weight	Testis width	Testis length	Percentage sperm	Percentage lumen	Tubule diameter
LH, overall mean	.46**	.26†	.49**	.45**	.27†	.24	.49**
42 d	.37*	.16	.43**	.33*	.22	.31*	.27†
56 d	.60**	.42**	.59**	.52**	.43**	.39**	.66**
70 d	.12	.27†	.16	.23	-.01	-.04	.22
84 d	.38*	.37†	.31†	.24	.37*	.33*	.44**
98 d	.06	.11	.13	.16	.10	.10	.16
112 d	.0	-.19	.0	.0	.04	.03	.03
126 d	.06	.07	.04	.10	-.10	-.18	-.09
140 d	-.13	.13	-.01	-.11	-.20	-.11	-.08
Maximum predicted LH concentration	.26†	.26	.31*	.35*	.20	.19	.42**
Age at maximum predicted LH concentration	-.10	-.16	-.17	-.13	-.12	-.15	-.26†
Variance of the LH samples	-.14	-.11	-.07	-.01	-.12	-.04	-.08
No. of peaks	.43**	.36*	.42**	.41**	.34*	.34*	.31†
FSH	-.14	.19	-.12	-.09	-.20	-.17	-.14

^aCorrelations pooled within line and farrowing group (36 boars).

^bLH = serum luteinizing hormone concentrations; no. of peaks = number of LH peaks observed from 42 to 140 d of age; FSH = mean concentration of follicle-stimulating hormone from 42 to 140 d of age.

^cPercentage sperm = percentage of seminiferous tubules with active spermatogenesis; percentage lumen = percentage of seminiferous tubules with a lumen; tubule diameter = seminiferous tubule diameter.

†P<.10.

*P<.05.

**P<.01.

TABLE 4. CORRELATIONS OF TESTICULAR TRAITS AND CONCENTRATIONS OF GONADOTROPINS WITH MEAN CONCENTRATIONS OF STEROIDS^a

Item ^b	Estradiol-17 β	Testosterone
Testis weight	.39**	.20
Epididymis weight	.41**	.33
Testis width	.31 [†]	.20
Testis length	.30 [†]	.18
Percentage sperm	.37*	.23
Percentage lumen	.22	.23
Tubule diameter	.40**	.12
LH concentration	.17	-.04
Maximum predicted		
LH concentration	.11	-.09
Age at maximum predicted		
LH concentration	-.23	.18
Variance of the		
LH samples	.23	.08
No. of peaks	-.08	.20
FSH	-.01	.04
Testosterone	.22	

^aPooled within line and farrowing group (36 boars).

^bPercentage sperm = percentage of seminiferous tubules with active spermatogenesis; percentage lumen = percentage of seminiferous tubules with a lumen; tubule diameter = seminiferous tubule diameter; no. of peaks = number of peaks observed from 42 to 140 d of age; FSH = mean concentration of follicle-stimulating hormone from 42 to 140 d of age.

[†]P < .10.

*P < .05.

**P < .01.

tubules with active spermatogenesis. Correlations between testis weight and testis sperm numbers in 210- to 225-d-old boars have been reported to be in the range of .65 to .91 (Wilson et al., 1977; Fent, 1980; Nelssen et al., 1982). In yearling bulls, correlations of scrotal circumference with sperm output and sperm concentration have been estimated to be .81 and .54, respectively (Hahn et al., 1969; Knights et al., 1982).

Correlations of body weight with epididymis weight and testis length were significant. The correlation of body weight with testis weight ($r = .13$) was smaller than those previously reported ($r = .5$ to $.7$; Allrich et al., 1982; Schinckel et al., 1983). The small, positive correlations found in this study between testis size and backfat thickness were similar to those found by Schinckel et al. (1983).

The majority of the correlations among levels of gonadotropins are small, suggesting that they are essentially independent. The observed correlation between the mean and maximum predicted LH concentrations is partially due to a part-whole relationship that

exists between the traits.

The two measures of variability, LH sample variance and number of peaks, were expected to be positively correlated. However, the correlation was low ($-.13$). The number of peaks is an estimate of the number of statistically significant releases of LH, but may not be equal to the number of LH releases that have physiological significance. At present, the magnitude of LH pulses required for modification of testicular function in the boar is not known. The sample variance estimates dispersion more precisely than the number of peaks, but may not be as biologically descriptive.

Boars with larger, more mature testes tended to have higher LH concentrations during development. In rams, within line correlations ranging from .5 to .7 have been found between testis diameter and mean LH concentrations when blood samples were taken 3 to 6 wk before the measurement of testis size (Carr and Land, 1975).

The concentrations of LH from 42 to 84 d of age were more highly correlated with testicular development than were LH concentrations

from 98 to 140 d. One possible explanation is that the increase in LH concentrations precedes the period of most rapid testicular development and that high LH concentrations from 42 to 84 d of age are indicative of boars with earlier and higher pubertal releases of LH, resulting in more fully developed testes at 140 d of age. In the present study, boars reached their maximum LH concentrations between 84 and 112 d of age, but rapid testicular development did not occur in this line until 120 to 160 d (Schinckel et al., 1983). A pubertal rise in LH concentrations that preceded testicular growth by several weeks was also found in bulls and rams (Lee et al., 1976; Lincoln et al., 1977; Lacroix and Pelletier, 1979). These results suggest that to determine biological relationships, blood samples should be taken before the measurement of testis growth and that correlations between testis growth and LH concentrations obtained at the same age should be interpreted with caution.

The correlations between the number of LH peaks and testis size suggest that the number of LH peaks may be related to pubertal development. Results of research conducted with rams and bulls also support the importance of a pulsatile pattern of LH release. Prolonged pulsatile infusion of luteinizing hormone-releasing hormone (LHRH, 100 or 500 ng iv/2 h) in intact rams during the nonbreeding season increased pulse frequency and mean concentrations of LH and resulted in increased growth of the testis (Lincoln, 1979). Also, ranks of breed means for age at puberty of rams and mean plasma LH concentrations, frequency of LH pulses and testis size were similar (Carr and Land, 1975).

Our results suggest that the variation among boars in testicular development and serum steroid concentrations cannot be explained by variation in FSH concentrations. Perhaps testicular growth and steroid production are not highly sensitive to normal physiological variation in FSH concentrations. Boars may vary in their sensitivity to FSH. Certainly, FSH plays a major role in pubertal development in other species. In the rat, FSH causes Leydig cell maturation, the conversion of T to E₂ and the production of androgen-binding protein (Bartke et al., 1978; Dorrington et al., 1978). In hypophysectomized rams, FSH acts synergistically with LH to increase testis growth (Courot, 1970).

Boars with larger, more mature testes tended to have higher serum steroid concentrations during development. This relationship has at least two possible interpretations: (1) boars with larger testes at 140 d had larger testes with greater numbers of steroid-producing cells during development, or (2) boars with higher steroid concentrations are less sensitive to the negative feedback effects of T and E₂ at the hypothalamo-hypophyseal axis, consequently their testicular growth occurs more rapidly. The magnitude of these correlations ($r = .18$ to $.41$) suggests that variation in steroid concentrations is virtually independent of testis size.

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