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Fent, R. W.; Wettemann, R. P.; and Johnson, R. K., "BREED AND HETEROSIS EFFECTS ON TESTICULAR DEVELOPMENT AND ENDOCRINE FUNCTION OF PUBERAL BOARS" (1983). *Faculty Papers and Publications in Animal Science*. 25.

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BREED AND HETEROSIS EFFECTS ON TESTICULAR DEVELOPMENT AND ENDOCRINE FUNCTION OF PUBERAL BOARS^{1,2}

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Summary

Purebred and two-breed cross Duroc, Landrace, Spotted and Yorkshire boars were evaluated at 218 ± 6 d of age to determine the influence of breed on testicular development and on concentrations of luteinizing hormone (LH) and testosterone in blood serum after treatment with gonadotropin releasing hormone (GnRH). Concentrations of LH and testosterone were determined in serum samples obtained from the vena cava of 139 boars just before and 1, 2, 3 and 4 h after an im injection of $200 \mu\text{g}$ of GnRH. The right testes of 136 boars were removed and sperm numbers were determined in homogenates of testicular parenchymae, capita-corpora epididymides and caudae epididymides. Crossbred boars weighed 7 kg more ($P < .05$) than purebred boars. Testes, capita-corpora and caudae epididymides were heavier ($P < .01$) for crossbred boars (46.4 ± 10.8 , 3.8 ± 1.4 and 4.8 ± 1.4 g, respectively) than for purebred boars. Crossbred boars had more testicular sperm ($33.7 \pm 2.0 \times 10^9$ vs $25.4 \pm 2.3 \times 10^9$, $P < .01$), more capita-corpora epididymidal sperm ($28.9 \pm 1.7 \times 10^9$ vs 20.8 ± 2.1

$\times 10^9$, $P < .01$) and more caudae epididymidal sperm ($53.6 \pm 2.9 \times 10^9$ vs $43.8 \pm 3.8 \times 10^9$, $P < .05$) than purebred boars. Breed of boar influenced ($P < .05$) testicular weight, capita-corpora weight and sperm numbers and caudal weight and sperm numbers. Concentrations of LH and testosterone in serum were similar ($P > .10$) for crossbred and purebred boars at all but one sampling time. At 3 h after treatment with GnRH concentrations of LH were greater ($P < .05$) in crossbred than purebred boars and concentrations of testosterone were greater ($P < .05$) in crossbred than purebred boars at 4 h after GnRH. There was a significant breed \times time interaction for concentrations of LH and testosterone. Breed of boar influenced ($P < .05$) concentrations of LH at 1, 2 and 3 h after treatment with GnRH, and concentrations of testosterone were affected by breed at 2 and 4 h after treatment. However, breed of boar did not influence either LH or testosterone in serum before treatment with GnRH (0 h) and LH in serum at 4 h and testosterone in serum at 1 and 3 h after GnRH. These results indicate that breed of boars influences testicular characteristics and concentrations of testosterone and LH in serum after GnRH. Heterosis was detected for testicular and epididymidal weights and sperm numbers, but heterosis was not observed for concentrations of LH and testosterone in serum.

(Key Words: Boar, Luteinizing Hormone, Puberty, Testis, Testosterone.)

Introduction

Testicular development is usually more rapid for crossbred than for purebred boars. Crossbred boars surpassed the parental lines in testicular weight, epididymidal weight and stage of spermatogenesis (Hauser et al., 1952). Heterosis was observed for testicular weight, caudae epididymidal weight and total testicular sperm

¹ Journal Article 3894 of the Agr. Exp. Sta., Oklahoma State Univ., Stillwater.

² Appreciation is expressed to Dr. R. L. Hintz for assistance with the statistical analyses. The authors thank Dr. G. D. Niswender, Colorado State Univ. for supplying testosterone-3-BSA and porcine luteinizing hormone (LH) antisera; Dr. L. E. Reichert, Jr., Albany Medical College for supplying porcine LH; and Dr. R. Rippel, Abbott Laboratories, North Chicago, IL, for the gonadotropin releasing hormone (GnRH).

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Received August 10, 1981.

Accepted January 6, 1983.

numbers in 7.5-mo-old Duroc × Hampshire crossbred boars (Wilson et al., 1977). Similarly, at 5.5 mo of age, Duroc × Yorkshire crossbred boars had larger testes and epididymides and more total testicular sperm than purebreds (Neely et al., 1979).

Systemic quantities of luteinizing hormone (LH) and testosterone in boars fluctuate during a day (Brock and Wettemann, 1976; Claus and Gimenez, 1977; Kattesh et al., 1979). Injection of boars with gonadotropin releasing hormone (GnRH) causes increased concentrations of LH and testosterone in serum (Pomerantz et al., 1974; Brock and Wettemann, 1977; Welsh and Johnson, 1979). However, the effects of breed and heterosis on concentrations of LH and testosterone in serum have not been determined.

The objectives of this study were to determine the influence of breed and heterosis on testicular development of boars at 7 mo of age and to determine if breed or heterosis influences concentrations of LH and testosterone in systemic serum after treatment with GnRH.

Materials and Methods

Purebred and two-breed cross Duroc, Landrace, Spotted and Yorkshire boars were evaluated at 218 ± 6 d of age. One hundred thirty-six boars were castrated during four seasons (spring 1977, fall 1977, fall 1978 and spring 1979) and blood samples were obtained from 139 boars during five seasons (spring, 1978 in addition to the above; table 1). Spring season included March through May, and fall season included September through November. One hundred twenty boars were bled and castrated. The boars were produced as part of a crossbreeding experiment and at least four sires per breed were used each season. A minimum of one new sire was added each season to each breed and a total of eight to 10 sires of each breed were used.

Boars were raised in confinement and managed in groups of about 10 animals until 5.5 mo of age, when they were transferred to nongrassay lots (10 to 15 boars/pen). At 7 mo of age, they were transported approximately 5 km and placed in slatted floor pens (2.3 × 4 m) with two to four/pen. Ambient temperatures were between 20 and 26 C. Five days after relocation each boar was injected im with 200

TABLE 1. NUMBER OF BOARS OF EACH BREED TYPE THAT WERE CASTRATED AND BLED

Breed type	No. castrated	No. bled
Duroc (D)	13	14
Landrace (L)	9	10
Spotted (S)	12	12
Yorkshire (Y)	10	9
	44	45
DL	17	19
DS	16	17
DY	15	16
LS	14	13
LY	14	14
SY	16	15
	92	94
	136	139

µg of GnRH⁶ at 1800 h. Blood was obtained by puncture of the vena cava just before (0 h) and at 1, 2, 3 and 4 h after treatment. Each blood sample (40 ml) was placed in a centrifuge tube, cooled to 5 C and allowed to clot for 20 h, then centrifuged at $5,000 \times g$ for 15 min. Serum was decanted and stored at -20 C until LH and testosterone were quantified by validated radioimmunoassays (Hallford et al., 1975; Wettemann and Desjardins, 1979).

The day after blood samples were collected, boars were anesthetized with sodium thiopental and castrated, and the right testes and epididymides were evaluated. Testicular parenchymae, capita-corpora epididymides and caudae epididymides were weighed and homogenized in saline-triton-merthiolate solution (Amann and Lambiase, 1969), and sperm numbers were determined (Kirton et al., 1967). Body weights were obtained at castration.

Testicular and epididymidal characteristics were analyzed by least-squares procedures (Harvey, 1972). The model included breed group, season and the interaction. Breed of sire, breed of dam and heterosis effects were determined by similar analyses. Endocrine data were subjected to split-plot analyses of variance as described by Gill and Hafs (1971) with two between block treatments (breed, season) and one within block treatment (time after GnRH treatment). When a significant breed × time interaction was detected, an analysis of variance

⁶Abbott Laboratories, North Chicago, IL.

TABLE 2. INFLUENCE OF BREED TYPE ON TESTICULAR AND EPIDIDYMAL CHARACTERISTICS OF BOARS

Item	Testicular		Caput-corpora epididymidal		Caudae epididymidal	
	Wt ^a , g	Total sperm (X 10 ⁹)	Wt ^a , g	Total sperm ^b (X 10 ⁹)	Wt ^a , g	Total sperm (X 10 ⁹)
Duroc (D)	229.5 ± 15.5 ^c	21.9 ± 2.8	28.8 ± 2.6	19.4 ± 3.4	33.4 ± 2.4	49.9 ± 7.6
Landrace (L)	284.4 ± 16.9	30.0 ± 5.8	29.0 ± 2.0	25.1 ± 4.8	34.6 ± 2.8	56.3 ± 8.6
Spotted (S)	240.4 ± 16.9	27.1 ± 5.1	27.4 ± 2.2	23.1 ± 4.9	27.3 ± 2.3	39.0 ± 6.7
Yorkshire (Y)	235.5 ± 13.9	23.9 ± 5.5	26.3 ± 1.2	15.7 ± 3.8	29.9 ± 1.8	30.2 ± 6.1
Purebred mean	243.1 ± 8.3	25.4 ± 2.3	27.9 ± 1.1	20.8 ± 2.1	31.2 ± 1.2	43.8 ± 3.8
DL	272.3 ± 19.5	32.4 ± 7.8	29.5 ± 2.3	22.1 ± 3.7	36.2 ± 2.2	47.7 ± 8.0
DS	287.3 ± 17.2	31.8 ± 4.1	31.7 ± 4.1	30.6 ± 4.1	36.6 ± 2.2	55.8 ± 7.7
DY	306.4 ± 12.3	39.9 ± 2.7	36.8 ± 2.5	31.6 ± 3.4	41.4 ± 1.3	64.0 ± 5.7
LS	269.9 ± 16.0	28.5 ± 4.3	27.9 ± 2.5	27.0 ± 5.7	32.7 ± 1.9	46.6 ± 9.1
LY	293.4 ± 12.2	35.2 ± 3.4	30.3 ± 1.6	30.4 ± 3.5	32.8 ± 1.9	48.6 ± 5.5
SY	319.4 ± 11.9	34.5 ± 4.0	33.7 ± 1.4	32.5 ± 4.5	35.6 ± 1.5	58.7 ± 6.5
Crossbred mean	291.5 ± 6.4	33.7 ± 2.0	31.7 ± .9	28.9 ± 1.7	36.0 ± .8	53.6 ± 2.9
Overall mean	276.5 ± 5.0	31.0 ± 1.5	30.5 ± .6	26.3 ± 1.2	34.4 ± .7	50.4 ± 2.2
Crossbred-purebred	46.4 ± 10.8**	8.3 ± 3.2**	3.8 ± 1.4**	8.1 ± 2.7**	4.8 ± 1.4**	9.8 ± 4.9*

^aEffect (P<.01) of breed type.

^bEffect (P<.05) of breed type.

^c $\bar{X} \pm SE$.

*P<.05.

**P<.01.

was utilized to evaluate breed effect within a breeding time. Correlations among traits were obtained within season and breedtype from corrected sums of squares and cross products pooled across subclasses.

Results and Discussion

Testicular and Epididymidal Characteristics. Season significantly influenced capita-corpora epididymidal weight, total testicular sperm, total capita-corpora epididymidal sperm and total caudae epididymidal sperm. Although season effects were noted, none of the breed \times season interactions were significant. Some of the seasonal differences may have been related to laboratory technique. Wilson et al. (1977) and Eden et al. (1978) also noted significant season effects for some testicular and epididymidal characteristics of 7.5- and 5.5-mo-old boars.

Breed of sire significantly influenced capita-corpora epididymidal weight and breed of dam influenced body weight and cauda epididymidal weight. Similarly, Wilson et al. (1977) found that breed of sire affected testicular, capita-corpora and caudae epididymidal weights in 7.5-mo-old boars.

Significant breed group effects were found for testicular weight, capita-corpora epididymidal weight and sperm numbers and caudae epididymidal weight and sperm numbers (table

2). Partial correlation coefficients (table 3) indicated that testicular and epididymidal weights were related to body weight.

Testes of crossbred boars were 19% heavier ($P < .01$) than testes of purebred boars (table 2). Previous studies indicated 30% (Hauser et al., 1952), 28% (Neely et al., 1979) and 16% (Wilson et al., 1977) heterosis for testicular weight in crossbred puberal boars. Crossbred boars also had 33% more ($P < .01$) testicular sperm than purebred boars. Similarly, Wilson et al. (1977) and Neely et al. (1979) observed that crossbred boars had 25 and 34% more testicular sperm, respectively, than purebred boars at 7.5 and 5.5 mo of age.

Capita-corpora epididymides of crossbred boars were 14% heavier ($P < .01$) and contained 39% more ($P < .01$) sperm cells than those of purebred boars (table 2). Neely et al. (1979) indicated large positive heterosis effects for total capita epididymidal sperm numbers in 5.5-mo-old boars. In contrast, crossbred and purebred Duroc and Hampshire boars had similar capita-corpora epididymidal weights and sperm numbers at 7.5 mo of age (Wilson et al., 1977).

Caudae epididymides of crossbred boars were 15% heavier ($P < .01$) and contained 22% more ($P < .05$) sperm cells than those of purebred boars. Wilson et al. (1977) found that crossbred boars had 8% heavier caudae epididymides, but that numbers of sperm in the caudae epididy-

TABLE 3. PARTIAL CORRELATION COEFFICIENTS FOR TESTICULAR AND EPIDIDYMIDAL CHARACTERISTICS OF BOARS

Item	TW ^b	CCEW ^c	CEW ^d	TSE ^e	CCES ^f	CESE ^g
BW ^a	.32	.34	.30	.10 ^h	.14 ^h	.14 ^h
TW ^b		.71	.66	.50	.53	.54
CCEW ^c			.65	.27	.58	.44
CEW ^d				.38	.47	.71
TSE ^e					.45	.40
CCES ^f						.50

^aBody weight.

^bTesticular weight.

^cCapita-corpora epididymidal weight.

^dCaudae epididymidal weight.

^eTesticular sperm number.

^fCapita-corpora epididymidal sperm number.

^gCaudae epididymidal sperm number.

^h $P > .05$; all other correlations are significant ($P < .05$).

mides were similar for purebred and crossbred boars at 7.5 mo of age. Neely et al. (1979) indicated negative heterosis for caudae epididymidal sperm numbers in 5.5-mo-old boars. Different management and age of boars at castration might influence ejaculation frequency in boars, thus affecting caudae epididymidal sperm numbers.

Partial correlations between the testicular and epididymidal characteristics (table 3) were all positive, and all were significant, except those between body weight and testicular, capitacorpora epididymidal and caudae epididymidal sperm numbers. Wilson et al. (1977) found significant positive correlations between most testicular and epididymidal characteristics of 7.5-mo-old boars. Testicular weights were also correlated with testicular sperm numbers in mature bulls (Almquist and Amann, 1961) and in mice (Johnson and Eisen, 1975).

Concentrations of Luteinizing Hormone and Testosterone in Systemic Serum after Treatment with Gonadotropin Releasing Hormone. Concentrations of LH and testosterone in serum of all boars (n = 139) increased after treatment with 200 µg GnRH (tables 4 and 5). Concentrations of LH in serum before treatment with GnRH averaged $1.6 \pm .1$ ng/ml and in-

creased to a maximum of $7.7 \pm .3$ ng/ml at 1 h after injection. Then concentrations of LH decreased to $2.0 \pm .1$ ng/ml by 4 h after treatment. Similar responses to treatment with GnRH have been reported for boars (Pomerantz et al., 1974; Brock and Wettemann, 1977; Welsh and Johnson, 1979).

Concentration of testosterone in serum averaged $3.2 \pm .2$ ng/ml before treatment (table 5). Testosterone in serum increased to $8.9 \pm .5$ ng/ml by 1 h after treatment with GnRH, and attained a maximum concentration of $13.8 \pm .8$ ng/ml by 2 h. By 4 h after treatment, concentrations of testosterone decreased to $8.5 \pm .4$ ng/ml.

Split-plot analyses indicated significant breed × time interactions for concentrations of LH ($P < .005$) and testosterone ($P < .001$), but breed × season interactions for LH and testosterone were not significant. Analyses of variance at each hour revealed that concentrations of LH were significantly influenced by season only at 1 h after treatment with GnRH. However, concentrations of testosterone were significantly influenced by season just before, and at 1 and 2 h after GnRH. None of the breed × season interactions was significant for concentrations of LH; however, breed × season interactions

TABLE 4. LUTEINIZING HORMONE (NG/ML)^a IN SYSTEMIC SERUM AFTER TREATMENT OF PUBERAL BOARS WITH GONADOTROPIN RELEASING HORMONE

Breed type	Time after GnRH treatment, h				
	0	1 ^b	2 ^b	3 ^c	4
Duroc (D)	$1.6 \pm .2^d$	9.4 ± 1.1	$6.8 \pm .9$	$3.8 \pm .6$	$2.3 \pm .3$
Landrace (L)	$1.7 \pm .2$	7.6 ± 1.1	5.8 ± 1.2	$2.9 \pm .6$	$1.9 \pm .3$
Spotted (S)	$1.5 \pm .2$	$6.3 \pm .8$	$4.3 \pm .6$	$2.4 \pm .3$	$1.5 \pm .1$
Yorkshire (Y)	$1.3 \pm .2$	$5.8 \pm .7$	$4.3 \pm .6$	$2.4 \pm .3$	$1.6 \pm .1$
Purebred mean	$1.5 \pm .1$	$7.4 \pm .5$	$5.4 \pm .4$	$2.9 \pm .2$	$1.9 \pm .1$
DL	$1.8 \pm .3$	$8.0 \pm .8$	$5.9 \pm .5$	$3.4 \pm .4$	$2.1 \pm .3$
DS	$1.7 \pm .2$	$8.4 \pm .9$	$6.2 \pm .6$	$3.8 \pm .4$	$2.1 \pm .2$
DY	$1.3 \pm .1$	$6.4 \pm .7$	$5.2 \pm .5$	$2.9 \pm .3$	$1.9 \pm .2$
LS	$1.7 \pm .1$	11.6 ± 2.1	8.1 ± 1.2	$4.0 \pm .5$	$2.2 \pm .2$
LY	$1.3 \pm .1$	$6.2 \pm .7$	$4.4 \pm .5$	$2.6 \pm .3$	$1.7 \pm .2$
SY	$1.5 \pm .1$	$6.6 \pm .7$	$5.0 \pm .6$	$2.9 \pm .3$	$1.8 \pm .2$
Crossbred mean	$1.6 \pm .1$	$7.8 \pm .4$	$5.8 \pm .3$	$3.3 \pm .2$	$2.0 \pm .1$
Overall mean	$1.6 \pm .1$	$7.7 \pm .3$	$5.6 \pm .2$	$3.2 \pm .1$	$2.0 \pm .1$

^aPorcine LH standard was LER-786-3.

^bEffect ($P < .01$) of breed type.

^cEffect ($P < .05$) of breed type.

^dMean ± SE.

were significant for concentrations of testosterone at 3 and 4 h after treatment. The cause of seasonal differences in testosterone is uncertain, but may be related to duration of photoperiod. Boars exposed to 16 h of light daily during growth have greater concentrations of testosterone in serum than boars exposed to 8 h of light (J. E. Minton, R. W. Fent and R. P. Wettemann, unpublished data).

Breed of sire influenced concentrations of LH at 1 h after GnRH and testosterone in serum at 2 and 4 h after GnRH. In addition, breed of dam significantly affected LH at all sampling times and testosterone at 1 h after treatment.

Concentrations of LH in serum of crossbred and purebred boars were similar, except at 3 h after treatment with GnRH, when crossbred boars had greater ($P < .05$) concentrations than purebred boars. Crossbred and purebred boars also had similar concentrations of testosterone except at 4 h after treatment (table 5). More frequent sampling of blood after treatment with GnRH may be necessary to study heterosis for reproductive hormones in boars.

Breed type did not significantly affect concentrations of LH in serum before or at 4 h after treatment with GnRH; however, breed

type did influence ($P < .05$) LH in serum at 1, 2 and 3 h after treatment (table 4). Concentrations of testosterone were not affected ($P > .10$) by breed type just before and at 1 and 3 h after GnRH (table 5). However, concentrations of testosterone were influenced ($P < .01$) by breed type at 2 and 4 h after GnRH. Breed \times season interactions were significant for testosterone at 3 and 4 h after treatment with GnRH. These data indicate that different breeds of boars may secrete different quantities of LH and testosterone in response to injection with GnRH, or that clearance rate of testosterone and LH from the blood may be influenced by breed. In either case, this experiment illustrates the need to consider breed of boars when studying factors that may influence testicular function.

General Discussion

The present results demonstrate the effect of breed type on testicular and epididymal weights and total epididymal sperm. Similar to previous studies (Wilson et al., 1977; Neely et al., 1979), the testes of crossbred boars were 19% heavier and contained 33% more sperm. The increased growth of the testes of crossbred boars compared with purebred boars suggests

TABLE 5. TESTOSTERONE (NG/ML) IN SYSTEMIC SERUM AFTER TREATMENT OF PUBERAL BOARS WITH GONADOTROPIN RELEASING HORMONE

Breed type	Time after GnRH treatment, h				
	0	1	2 ^a	3 ^b	4 ^{ab}
Duroc (S)	3.1 \pm .6 ^c	10.4 \pm 3.5	9.3 \pm 1.2	9.2 \pm 1.4	6.2 \pm 1.2
Landrace (L)	2.9 \pm .7	7.5 \pm 1.4	15.9 \pm 2.5	13.4 \pm 2.3	7.1 \pm 1.2
Spotted (S)	2.1 \pm .4	6.1 \pm .8	11.6 \pm 1.4	11.2 \pm 2.6	5.4 \pm 1.0
Yorkshire (Y)	4.0 \pm 1.0	12.4 \pm 2.8	26.0 \pm 7.6	15.2 \pm 3.5	9.4 \pm 2.2
Purebred mean	2.8 \pm .3	9.0 \pm 1.3	14.7 \pm 1.9	11.9 \pm 1.2	6.9 \pm .7
DL	3.2 \pm .7	7.7 \pm 1.1	11.2 \pm 1.3	10.2 \pm 1.0	8.8 \pm 1.3
DS	4.3 \pm 1.0	8.9 \pm 1.6	10.8 \pm 1.4	9.7 \pm 1.4	8.4 \pm 1.5
DY	3.5 \pm .6	11.3 \pm 1.8	14.9 \pm 1.5	13.8 \pm 1.6	12.3 \pm 2.5
LS	2.2 \pm .6	6.5 \pm 1.1	11.3 \pm 1.3	9.7 \pm 1.3	7.1 \pm .7
LY	2.5 \pm .5	8.8 \pm 1.4	13.2 \pm 1.8	12.3 \pm 1.9	7.5 \pm 1.3
SY	3.7 \pm .5	9.5 \pm .9	18.9 \pm 4.7	13.9 \pm 1.7	11.0 \pm 1.3
Crossbred mean	3.3 \pm .3	8.8 \pm .6	13.3 \pm 1.0	11.6 \pm .6	9.3 \pm .7
Overall mean	3.2 \pm .2	8.9 \pm .5	13.8 \pm .8	11.7 \pm .5	8.5 \pm .4

^aEffect ($P < .01$) of breed type.

^bBreed \times season interaction ($P < .05$).

^cMean \pm SE.

that increased amounts of gonadotropins are secreted by crossbred boars and(or) the testes of crossbred boars are more responsive to gonadotropins.

Heterosis was not observed for concentrations of LH in systemic serum before treatment of boars with GnRH and concentrations of LH were similar in purebred and crossbred boars at all sampling periods after GnRH except at 3 h. Although breed type did not affect concentration of LH before GnRH, LH was influenced by breed type at 1, 2 and 3 h after GnRH. The lack of a breed effect on LH before GnRH is probably related to much variation in serum LH caused by fluctuating concentrations in boars during a day (Brock and Wettemann, 1976). The coefficient of variation for LH concentrations in the serum of boars can be reduced by treatment with GnRH (Brock and Wettemann, 1977). Treatment of boars in this study with 200 µg GnRH allowed comparison of the amounts of releasable LH in boars of different breeds. Thus it appears that LH secretion cannot be increased by crossbreeding, but it can be increased by selection of the breed of boar.

Breed type significantly influenced concentrations of testosterone in serum at 2 and 4 h after GnRH. The absence of a breed type effect on serum testosterone at 0, 1 and 3 h after GnRH is probably related to much variation in serum testosterone caused by fluctuating concentrations of testosterone in boars during a day (Brock and Wettemann, 1976; Fonda et al., 1981). In agreement with a lack of heterosis for serum LH, crossbred and purebred boars had similar concentrations of testosterone in serum except at 4 h after GnRH.

The present failure to detect heterosis for serum LH and testosterone in boars and yet observe an unequivocal influence of heterosis on testicular and epididymal weights and sperm numbers suggests that the gene action for endocrine function is different than that for testicular and epididymal weights and sperm numbers. Taken together the influence of breed type on testicular weight, epididymal weight and total sperm, and serum LH and testosterone after GnRH establishes that genotype regulates testicular and reproductive endocrine function in boars. The present findings support the proposition that breed type alters sperm production, as well as concentrations of LH and testosterone in the serum of boars and these alterations may be related to reproductive efficiency.

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