RELATIONSHIPS OF REPRODUCTIVE TRAITS AMONG LITTERMATES IN SWINE

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CHAPTER I

INTRODUCTION

Changes in livestock production can be brought about by either changes in the environment or manipulation of the genotypes of the animals involved. Environmental changes are generally only temporary, while genetic changes are relatively permanent. Changes in the genotype can be accomplished by selecting for a desirable phenotype among animals retained for mating. The problem that arises is that some traits are not expressed in both the male and the female. This makes it difficult to be able to select animals that will pass on desirable genes to their offspring for a particular trait, when the parent does not express this trait directly. In the dairy industry it often takes five to six years to identify a sire that passes on desirable genes to his daughters for milk production. This practice of progeny testing can only be economically feasible when germ plasm from superior sires can be marketed on an extensive program through artificial insemination. For species that do not and cannot utilize progeny testing on such a large scale, the intuitive way to approach this problem would be to identify a trait or traits in one sex that are being controlled by genes similar to those

controlling the trait or traits in the sex of interest. In this fashion a majority of the superior parents may be identified on their own merit.

It has been postulated that sexual activity and reproductive function in males and females may be correlated genetically (Land, 1973). This is due to the fact that the same gonadotrophic hormones control reproductive and sexual activity in both sexes. Studies in mice have shown that selection for ovulation rate in the female will cause a highly positive correlated response in testis weight of male sibs (Land, 1973). Islam et al. (1976) found a moderate positive correlated response for ovulation rate in females when lines of mice were selected for testis weight. It has been documented in sheep that in breeds that are noted for female reproductive prolificacy, males had higher concentrations of plasma luteinizing hormone and greater testis growth at young ages (Land, 1973; Land and Carr, 1975). In an attempt to determine if producers could select bulls that will reduce age at puberty in their heifer offspring, Brinks et al. (1978) found a genetic correlation of -0.71 among half-sibs for age at puberty in heifers and scrotal circumference. Schinckel (1980), working with Nebraska gene pool population, reported that in swine the correlation between ovulation rate and excised testis weight may be as low as 0.20. The purpose of this study is two-fold: 1. to approximate the relationship of a boar's testicular and reproductive traits with the age and weight

at puberty of his full-sib sisters; and 2. to calculate heritability estimates of boar testicular and reproductive traits.

CHAPTER II

REVIEW OF LITERATURE

Introduction

The following is a review of heritability estimates, correlation coefficients and the effects of crossbreeding for male and female reproductive traits in swine. This is necessary to better understand the genetic inheritance of reproductive traits. With this information accurate recommendations can be made about the expectation for improvement of these traits by selection or crossbreeding programs.

When appropriate, summaries and weighted averages of parameter estimates are presented in tabular form. Heritability and correlation estimates are influenced by breed composition of the experimental animals and method of computation. To better understand the literature estimates presented in the summary tables, a listing of abbreviations of terms, breeds and traits used in these tables is presented in Table I.

TABLE I

SUMMARY OF SYMBOLS AND ABBREVIATIONS USED IN HERITABILITY AND CORRELATION SUMMARY TABLES

General abbreviations and symbols

CI - Corrected for inbreeding
h^2 - Heritability
N_L - Number of litters in the study
N_P - Number of progeny in the study
N_S - Number of sires used in the study
r_g - Genetic correlation
r_p - Phenotypic correlation
SE - Standard error of the estimate

Abbreviations used to describe the breed or line

CO - Cornwall
COL - Control line composed of several breeds
D - Duroc
DN - Danish
DL - Danish Landrace
FO - Foundation stock for Minnesota No. 1 and Minnesota No. 2
H - Hampshire
HP - Line selected for high growth rate and low backfat
IDL - Inbred Nebraska Duroc lines
IL - Inbred line records from Regional Swine Breeding Laboratory
JAS - Jersey Angeln Saddleback
KG - Control line
LCS - Line selected for improvement of carcass score
LFE - Line selected for improvement of feed efficiency
LI - Line selected for improvement of index score
LN - Landrace
LP - Line selected for high growth rate and low backfat
LW - Large White
M - Managra
MO#1 - Montana No. 1
MY - Middle Yorkshire
M #1 - Minnesota Number One
M #2 - Minnesota Number Two
M #3 - Minnesota Number Three
M #4 - Minnesota Number Four
NGPP - Nebraska Gene Pool Population
PC - Poland China
SP - Spotted
UR - Urzhum

TABLE I (Continued)

Abbreviations used to describe the breed or line - Continued

XB - Animals involved were crossbred, e.g., XB (D, Y, LN + SP) refers to swine that were Duroc, Yorkshire, Landrace and Spotted crossbreeds.
Y - Yorkshire

Abbreviations of methods used to obtain heritability and correlation estimates

FSC - Full-sib correlation
ISROD - Intra-sire regression of offspring on dam
MethI, UW - Realized estimate procedure regressing response on cumulative selection differential
MethI, W - Weighted realized estimates of Method I
MethII, UW - Realized estimate procedure using the ratio of the sum of the yearly deviations weighted by the year number to the sum of squares of the number
MethII, W - Weighted realized estimates using Method II
MethIII, UW - Realized estimate procedure using the ratio of the line difference in the last generation to the cumulative selection differential
MethIII, W - Weighted realized estimates using Method III
MHS - Maternal half-sib correlation
REAL - Realized estimates obtained from selection experiments
ROD - Regression of offspring on dam
RODG - Regression of offspring on granddam
PHS - Paternal half-sib correlation
SVCC - Calculated from the sire of the dam variance component

Abbreviations of traits considered in the summary of heritability estimates and correlations

AGP - Age at puberty of gilts
CL/EM - Number of corpora lutea per normal embryos in pregnant gilts
EM/GL - Number of normal embryos per corpora in pregnant gilts
LBW - Litter birth weight
LGAP - Average of all gilts in the litter of the gilt being studied for age at puberty
LGWP - Average of all gilts in the litter of the gilt being studied for weight at puberty

TABLE I (Continued)

Abbreviations of traits considered in the summary of heritability estimates and correlations - Continued

LSBG - Number of pigs born alive in the litter of the gilt being studied
NB - Total number of pigs born in the litter
NBA - Total number of pigs born alive in the litter
PLECL - Percentage of live embryos of corpora lutea
P.LH - Plasma Luteinizing Hormone
P.Prog - Plasma Progesterone

A Summary of Heritability and Correlation Estimates for Female Reproductive Traits

Litter Size at Birth

There are two ways that litter size at birth can be expressed: total number of pigs born, and number of pigs born alive. Published heritability estimates for number born and number born alive ranged from -0.06 to 0.72 and 0.07 to 0.66, respectively (Table II). Weighted average heritability estimates for number of pigs born and number of pigs born alive were 0.109 and 0.105, respectively. This indicates that the variation in these two traits is largely due to non-additive gene effects and the environment. Urban et al. (1966) suggested that there is an uncorrectable maternal effect of the dam on the daughter's litter size. In their study, condition of the sow had a greater effect on mortality than did number of pigs farrowed. Sows that were in poor condition would not be able to provide an optimum maternal environment, thus affecting the future performance of her litter. They further reported that the heritabilities of litter size for different size litters are different. The heritability for litters of seven or more pigs was 0.12, while the heritability for all litters was 0.08. The explanation for this may be that a negative phenotypic correlation exists between the body weight of a dam and the litter size in which she was born. Dams which

TABLE II

SUMMARY OF HERITABILITY ESTIMATES FOR
NUMBER BORN AND NUMBER BORN ALIVE

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Stewart, H. A., 1945				FD,M#1,M#2	ROD	.150 .132	±.114 ±.113	NB NBA
Krider et al., 1946	741	98	41	H	PHS	.046		
Blunn and Baker, 1949	561			IDL	ISROD	.251 .237		NB NBA
Boylan et al., 1961				M#1 M#2 M#3 M#4	ROD ROD ROD ROD	.05 .04 .17 .03	±.13 ±.10 ±.14 ±.07	NBA NBA NBA NBA
Abarca, V., 1963				LN,D,JAS		.10		
Jensen, P., 1965		595		DL	ISROD	.20 .28		NB NBA
Noland et al., 1966	3360	411		PC	PHS	.11	±.23	NBA
Simoni et al., 1966	733	121	15	LW,LN		.12		

TABLE II (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Stockhausen and Boylan, 1966		304*		M	PHS	.59	±.29	NBA
					ROD	.26	±.15	NBA
Urban et al., 1966	35,891	3119		IL	ROD	.09	±.04	NB
						.08	±.04	NBA
Jenson, P., 1967		540		DA		.11	±.09	
Louca and Robison, 1967	8039	1396	76	D,Y	ROD	.05	±.20	
		245*		XB (D,Y)				
Fiedler et al., 1969				CO		.17		NBA
Gruden and Nikitcenco, 1969		640		UR		.281		
Nikolic et al., 1969		411		DL		.226		
Vangelov, K., 1969	10,309			LW		.17		
Edwards and Omtvedt, 1970	3760	202*		COL	ROD	.01	±.14	
Legault, C., 1970		11266	886	LW		.006		

TABLE II (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Biederman et al., 1971		1070		LN		.39		
Fahmy and Bernard, 1972		751		LFE,LCS, LI	PHS	.24		NB
					ROD	-.06		NB
					PHS	.24		NBA
					ROD	-.07		NBA
Morris, C. A., 1973		8492			PHS	.07	±.04	
Ollivier, L., 1973				LW		.39		
Revelle and Robison, 1973		750		D,Y	ROD	.13	±.06	NBA
Arganosa et al., 1974/75		737	231	D,Y,LN	PHS	.19	±.12	NB
					PHS	.16	±.12	NBA
Baik et al., 1974	5547	614		MY	PHS	.25	±.03	
Cummings et al., 1974				M#1	ROD	.188	±.135	
				M#2	ROD	.217		CI
Eikjie, D., 1974		38,278			PHS	.19	±.07	NBA
					FSC	.14	±.04	NBA

TABLE II (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Johar et al., 1974		282	19	MY	PHS	.25	±.03	
Irvin, K. M., 1975		609		Y,D,H	PHS	.26		NB
						.20		NBA
Baharin and Beillarz, 1977		9220	308	LW,LN XB (LW,LN)	PHS	.07	±.02	
Young et al., 1977		531		D,Y,H XB (D,Y,H)	PHS	-.05	±.18	NBA
Young et al., 1978		2095	295	NGPP	PHS	.33	±.26	NBA[3]
						.72	±.22	NB[4]
						.66	±.23	NBA[4]
Strang and King, 1979		38,000	146	LW	PHS	.04	±.04	NBA
					ROD	.07	±.02	NBA
		35,000	860	LN	PHS	.07	±.03	NBA
					ROD	.09		NBA
Pumfrey et al., 1980		789		NGPP	PHS	.47	±.21	NB
					FSC	.17	±.14	NB
					PHS	.44	±.21	NBA
					FSC	.16	±.14	NBA

TABLE II (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Vangen, O., 1980		2150		LP,HP,KG	PHS	.04	±.04	NB[1]
						.00	±.18	NBA[1]
						.28	±.30	NB[2]
						.26	±.30	NBA[2]
Gaugler, H. R.,		366	41	Y,SP,LN,D	PHS	.36		NB
				Weighted Average, NB		.109	(21 estimates)	
				Weighted Average, NBA		.105	(16 estimates)	

*Number of daughter-dam pairs

[1]Based on first litter records

[2]Based on the average of the dam's first two litters

[3]Based on the record of the litter in which the gilt was born

[4]Based on the litter the gilt produced

were born in smaller litters had a more favorable environment. due to reduced competition; thus they would produce litters larger than their genetic capability. Similar findings were reported by Revelle and Robison (1973). It has been hypothesized that a negative genetic covariance between direct and maternal effects may be important in the expression of a gilt's first litter record, and thus influence the expression of her true breeding value (Revelle and Robison, 1973; Vangen, 1980b). However, this effect only influences the first litter (Vangen, 1980b).

Litter Weight at Birth

The heritability estimates for litter weight at birth ranged from 0.00 to 0.73 (Table III). The weighted average heritability was 0.261, suggesting that litter weight at birth is a low to moderately heritable trait.

Correlations among number born, number born alive, and litter birth weight are presented in Tables IV and V. The weighted average phenotypic correlation between number born and number born alive is large and positive (0.93). The weighted average genetic correlation is much lower (0.40) than the average phenotypic correlation, suggesting that non-additive genetic effects and environmental factors possibly influence the relationship of these two traits. The weighted average genetic and phenotypic correlations between number born alive and litter birth weight are both positive and of similar magnitude (0.84 and 0.89,

TABLE III

SUMMARY OF HERITABILITY ESTIMATES FOR LITTER BIRTH WEIGHT

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Krider, et al., 1946				M#1, M#2	ROD	.307 .355		CI
Arbarva, V., 1963				LN,D,JAS	ISROD	.12		
Jensen, P., 1965		595		DL	ISROD	.19		
Noland et al., 1966	3360	411		PC		.73	±.24	
Louca and Robison, 1967	8039	1396	76	D,Y XB (D,Y)	PHS PHS	.17 .05	±.42 ±.20	
Vangelov, K., 1969	10,309			LW		.18		
Edwards and Omtvedt, 1970	3760	202*		COL	ROD	.27	±.15	
Baik et al., 1974	5547	614		LN		.06		
Johar et al., 1974		282	19	MY	PHS	.08	±.02	

TABLE III (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	h^2	SE	Comment
Irvin, K. M., 1975		609		Y,H,D	PHS	.54		
Young et al., 1978		2095		NGPP	PHS	.29	±.23	
Pumfrey et al., 1980		789		NGPP	PHS	.26	±.20	
					FSC	-.00	±.15	
Gaugler, H. R., 1980		366	41	Y,D,SP,LN	PHS	.31		
				Weighted Average		.261	(10 estimates)	

*Number of daughter-dam pairs

TABLE IV

SUMMARY OF CORRELATION ESTIMATES OF NUMBER BORN WITH INDICATED TRAITS

Item	Edwards and Omtvedt 1970	Fahmy and Bernard 1972	Baik et al., 1974	Arganasa et al., 1974/75	Young et al., 1978	Average
N_P	3760		5547			
N_L	202*	751	614	737	2095	
N_S				231	295	
Breed or line	COL	Y	LW,LN, XB (LW,LN)	D,Y,LW	NGPP	
Method			PHS	PHS	PHS	
$NBAr_p$		.93		.91	.93	.93(3)[a]
$NBAr_g$			.19	>1.00	.96±.33	.40(2)
$LBWr_p$	.89	.81			.76	.84(3)
$LBWr_g$			.84		1.03±.48	.89(2)

*Number of dam-daughter pairs

[a]Number of estimates used in estimating weighted average

TABLE V

SUMMARY OF CORRELATION ESTIMATES OF NUMBER BORN ALIVE WITH LITTER BIRTH WEIGHT

Item	Fahmy and Bernard 1972	Baik et al., 1974	Young et al., 1978	Weighted Average
N_P		5547	2095	
N_L	751	614	295	
N_S				
Breed or Line	Y	LW, LN XB (LW,LN)	NGPP	
Method		PHS	PHS	
$LBWr_p$	.77		.84	.82(2)[a]
$LBWr_g$		.94	.92±.50	.93(2)

[a]Number of estimates used in estimating weighted average

respectively). Environmental effects and non-additive gene effects appear to have a smaller role in the relationship between these two traits and selection for one should generally result in improvement of the other. The correlations between number born alive and litter birth weight are similar to those for total number born and litter birth weight. All three of these traits are probably influenced by many of the same genes.

Ovulation Rate and Associated Traits

An early study reported that corpora lutea count had a heritability of 0.10 (Table VI; Lasley, 1957). This indicated that ovulation rate is a lowly heritable trait. However, realized heritability estimates from data collected from the Nebraska ovulation rate selection experiment indicated that it is moderately heritable (Zimmerman and Cunningham, 1975; Newton et al., 1977; Cunningham et al., 1979). Young et al. (1977b) reported an ovulation heritability estimate (.21) using the paternal half-sibs, which was intermediate to the other studies. On the other hand, several authors using the paternal half-sib correlation method reported heritability estimates as large or larger than the realized heritability estimates (Young, et al., 1978; Pumfrey et al., 1980; Wettemann et al., 1980). A summary of correlations of ovulation rate with other reproductive traits is provided in Table VII. The estimates are highly variable and difficult to interpret. Several

TABLE VI

SUMMARY OF HERITABILITY ESTIMATES OF OVULATION RATE

Author	N_P	N_L	N_S	Breed or Line	Method	L^2	SE	Comment
Lasely, E. L., 1957				PC,LN,D,Mo#1	PHS	.10		
Zimmerman and Cunningham, 1975				NGPP	MethI, UW	.48	±.09	Five generations of selection
					MethI, W	.52	±.10	
					MethII, UW	.36	±.07	
					MethII, W	.40	±.07	
					MethIII, UW	.41	±.06	
					MethIII, W	.45	±.07	
Newton et al., 1977				NGPP	MethI, UW	.37	±.09	Seven generations of selection
					MethI, W	.40	±.07	
					MethII, UW	.32	±.07	
					MethII, W	.35	±.06	
					MethIII, UW	.32	±.06	
					MethIII, W	.35	±.07	
Young et al., 1977b	531			D,Y,H XB (D,Y&H)	PHS	.21	±.20	
Young et al., 1978	2095			NGPP	PHS	.59	±.12	Eight generations of selection

TABLE VI (Continued)

Author	N_P	N_L	N_S	Breed or Line	Method	L^2	SE	Comment
Cunningham et al., 1979				NGPP	MethI, W	.42	±.06	Nine generations of selection
					MethII, W	.37	±.05	
					MethIII, W	.42	±.06	
Pumfrey et al., 1980				NGPP	PHS	.49	±.10	Ten generations of selection
					FSC	.51	±.06	
Wettemann et al., 1980	133			D,Y,H XB (D,Y&H)	PHS	.41	±.41	

TABLE VIII

SUMMARY OF CORRELATION ESTIMATES OF OVULATION RATE WITH OTHER TRAITS

Item	Robertson et al., 1951[a]	Warnick et al., 1951	Squires et al., 1952	Reddy et al., 1958	Newton et al., 1977	Young et al., 1977b	Young et al., 1978	Cunningham et al., 1979	Wetteman et al., 1980	Weighted Average
No	43	112		111	2161	531	2095		133	
N_L								781		
N_S							295			
Breed or Line	PC,DW	CW+Y	IPC,D IH	LN,PC XB (L,PC+D)	NGPP	D,Y,H XB (D,Y+H)	NGPP	NGPP	D,Y,H XB (D,Y+H)	
Method					REAL	PHS	PHS	REAL	PHS	
NB r_p			.49			-.03	.06			
NB r_g						Neg*	.01±.46	.07		
NBA r_p							.04	.11		
NBA r_g							.38±.51			
LBW r_p							.05			
LBW r_g							.88±.91	.18		

TABLE VII (Continued)

Item	Robert-son et al., 1951	War-nick et al., 1951	Squires et al., 1952	Reddy et al., 1958	Newton et al., 1977	Young et al., 1977b	Young et al., 1978	Cunningham et al., 1979	Wetteman et al., 1980	Weighted Average
LSBG r_p							.02			
LSBG r_g							.56			
AGP r_p	.19	-.24	.31		-.04		.12			.06(3)
AGP r_g							-.10			
WTP r_p	-.05				-.04		.27			.11(3)
WTP r_g							-.15			
LGAP r_p							.10			
LGAP r_g							-.13			
LGWP r_p							.19			
LBWP r_g							.21			
NNE r_p			.38				.41		.36	
NNE r_g							Neg		-	
CI/EM r_p						.21				

TABLE VII (Continued)

Item	Robert-son et al., 1951	War-nick et al., 1951	Squires et al., 1952	Reddy et al., 1958	Newton et al., 1977	Young et al., 1977b	Young et al., 1978	Cunningham et al., 1979	Wetteman et al., 1980	Weighted Average
CI/EM r_g						1.83				
EM/CL r_p						.26				
EM/CL r_g						Neg				
PLECL r_p									-.33	
PLECL r_g									$-1.45 \pm .73$	

*Sign of covariance

[a]Number of estimates utilized

authors evaluated ovulation rate for the second estrus cycle (Robertson et al., 1951; Newton et al., 1977; Young et al., 1977b; Young et al., 1978; Cunningham et al., 1979). Others determined ovulation rate for the first estrus cycle (Warnick et al., 1951; Squires et al., 1952). Still others determined ovulation rate in gilts that were slaughtered after breeding (Reddy et al., 1958; Wettemann et al., 1980).

The genetic relationship between ovulation rate and number born appears to be near zero. Phenotypic correlations of ovulation rate with age and weight at puberty are variable, and a weighted average correlation indicates that if a relationship does exist between ovulation rate and age and weight at puberty it is extremely small.

Results from 339 purebred Duroc, Hampshire and Yorkshire gilts, along with 192 two-breed crosses among these three breeds, indicate that the number of live embryos at 30 days of gestation had an estimated heritability of -0.39 ± 0.17 (Young et al., 1977b). In a similar study, 133 purebred and two-breed cross gilts of Duroc, Hampshire and Yorkshire breeding, had a heritability estimate of -0.21 ± 0.67 was reported for the number of embryos at 30 days postbreeding (Wettemann et al., 1980). This may indicate that the additive genetic variance is near zero. However, percent live embryos of corpora lutea was reported to have a heritability of 0.57 ± 0.41 (Wettemann et al., 1980). The ratio of the number of embryos to the number of corpora

lutea had a negative estimate for the sire component of variance. Its converse, the ratio of the number of corpora lutea to the number of embryos, had a positive estimate of the sire component of variance and a heritability value of 0.28±0.20 was reported (Young et al., 1977b). Correlations of various reproductive traits and number of embryos are presented in Table VIII. Phenotypic correlations ranged from -0.68 to 0.75. Genetic correlations could not be estimated. This coupled with the differences in traits between the two studies makes interpretation difficult.

Age and Weight at Puberty

Average heritability estimates for age and weight at puberty are 0.33 and 0.31, respectively (Table IX). It appears that moderate progress may be expected from selection for either of these traits. Estimates of the correlation between age and weight at puberty can be found in Table X. Weighted averages of the phenotypic and genetic correlations are positive and similar in magnitude (0.63 and 0.66, respectively). This suggests that non-additive gene effects and environmental factors have a smaller effect in the relationship of these two traits. It should be noted, however, that the authors presenting the genetic correlations between age and weight at puberty suggested these estimates were not significantly different from zero (Young et al., 1978; Hutchens, 1980).

TABLE VIII

SUMMARY OF CORRELATION ESTIMATES OF NUMBER OF NORMAL EMBRYOS WITH OTHER TRAITS

Item	Young et al., 1977b	Wettemann et al., 1980
No	531	133
N_L		
N_S		
Breed or Line	D,Y,H XB (D,Y+H)	D,Y,H XB (D,Y+H)
Method	PHS	PHS
PLECL r_p		.69
PLECL r_g		POS*
P.Prog r_p		.05
P.Prog r_g		POS
P.LH r_p		.17
P.LH r_g		POS
NB r_p	-.03	
NB r_g	Neg	
EM/CL r_p	.75	
EM/CL r_g	Neg	
CL/EM r_p	-.68	
CL/EM r_g	Neg	

*Sign of the covariance

TABLE IX

SUMMARY OF HERITABILITY ESTIMATES FOR AGE AND WEIGHT AT PUBERTY

Author	N_P	N_L	N_S	Breed or Line	Method	Age h^2	Age SE	Weight h^2	Weight SE
Reutzel and Sumption, 1968	1192	312	123	NGPP	PHS	-.20	±.14	.17	±.14
	800				ISROD	.49	±.11	.52	±.08
Legault, G., 1973	304		65	LN,LW	PHS	.46		.44	
Cunningham et al., 1974[a]	137			NGPP	ROD	.64	±.30		
	68			NGPP	ROD	-.28	±.36		
Pumfrey et al., 1975	1609			NGPP	ROD	.38	±.04	.34	±.06
Young et al., 1978[b]	2095		292	NGPP	PHS	.53	±.13	.27	±.12
Hutchens, L., 1980	737		32	D,Y,LN,SP,	PHS	.19	±.09	.35	±.12
				XB (D,Y,LN+SP)	MHS	.40	±.13	.26	±.12
				Weighted average		(.33)	(6)[c]	.31	(4)

[a]Estimates involved different samples.

[b]Pumfrey et al. (1975) analysis was from a portion of these data.

[c]Number in parentheses is the number of estimates utilized.

TABLE X

SUMMARY OF CORRELATION ESTIMATES BETWEEN AGE AND WEIGHT AT PUBERTY

Author	N_P	N_L	N_S	Breed or Line	Method	r_p	r_g
Phillips and Zeller, 1943	63			PC		-.51	
Gossett and Sorenson, 1959	52			D,H,PC		-.45	
Obannon et al., 1966	72			XB		.46	
Reutzel and Sumption, 1968	1192	312	123	NGPP	PHS	.62	
Young et al., 1978	2095		292	NGPP	PHS	.68	.90
Hutchens, L. 1980	737		32	D,Y,LN,SP	PHS	.54	-.03
				Weighted estimate		.63(6)[a]	.66(2)

[a]Number in parentheses is the number of estimates utilized.

Effects of Crossbreeding on Female Reproductive Traits

The use of crossbreeding as a tool to increase productivity has become an integrated portion of the swine industry. Crossbreeding's primary agent is that of heterosis or "hybrid vigor." Heterosis is the increased vigor or productivity of the crossbred offspring relative to the average of their purebred parents. Heterosis works through non-additive gene effects. Traits that are controlled primarily by additive gene pairs have little or no response to crossbreeding, however those traits that are not controlled by additive gene effects and thus will not respond readily to selection, should respond favorably to crossbreeding. Reproductive traits are generally lowly heritable and show considerable benefit from heterosis and crossbreeding.

Age and Weight at Puberty

Results from early crossbreeding experiments were actually reports of trials conducted to investigate the performance of offspring that were the results of crossing inbred lines. Age at breeding was found to decrease by 28 days when comparing line cross gilts to those of inbred lines of Poland China and Hampshire ancestry (Squires et al., 1952). In an experiment investigating characteristics of linecross and crossbred females, linecross females were

34.3 days younger at puberty than were gilts of the parental lines. However, a larger advantage was found with crossbred gilts that were 63.4 and 75.4 days younger at puberty than purebred and topcross offspring, respectively (Foote et al., 1956). Chester White and Poland China crossbred gilts were found to be 21.7 days younger than were the corresponding purebreds at puberty (Zimmerman et al., 1960). Clark et al. (1970) used Yorkshire and Poland China gilts and their reciprocal crosses and found that purebreds were significantly older ($P<.01$) than were the crossbred gilts (236 days versus 222 days at puberty). In a review paper summarizing work done in Europe and the United States, Sellier (1976) reported that for the five studies reviewed, crossbred gilts were an average of 18 days younger at puberty than the purebreds. In contrast, reciprocal cross females of Duroc, Spotted, Yorkshire and Landrace breeding were only 7.9 days younger than the purebreds (Hutchens, 1980). It has been suggested that the inheritance of age at puberty is largely non-additive (Foote et al., 1956; Zimmerman et al., 1960).

Few reports in the literature have tried to determine the effect of crossbreeding on weight at puberty. In a study using the Duroc and Yorkshire breeds, reciprocal cross gilts were 4.2 kg heavier at first estrus than were the purebreds (Short, 1963). In contrast, two-breed cross gilts of Spotted, Yorkshire, Duroc and Landrace ancestry were only 0.9 kg heavier than their purebred counterparts (Hutchens,

1980).

Ovulation Rate

The number of pigs born in a litter is a composite of several different traits, including ovulation rate. If ovulation rate would respond favorably to crossbreeding, then an increase in litter size would be a reasonable expectation. In a Missouri experiment, where inbred lines of Poland Chinas and Hampshires along with non-inbred Durocs and their reciprocal crosses were being studied, it was reported that crossbred gilts shed 1.19 more ova at ovulation than did the parental breeds (Squires et al., 1952). In contrast, Yorkshire and Hampshire reciprocal cross gilts showed no significant difference for ovulation rate (Rio, 1957). However, Yorkshire sired crossbred gilts shed more ova (2.06) than did crossbred gilts sired by Hampshires. Purebred and two-breed gilts of Hampshire, Duroc and Yorkshire breeding were evaluated, and crossbred gilts averaged 0.77 fewer corpora lutea at 30 days postbreeding than purebred gilts, however this difference was not significant (Johnson and Omtvedt, 1975). In a later paper involving the same study, Johnson et al. (1978) examined 148 purebred and 194 two-breed cross gilts and found that the ovulation rates were nearly identical. The inconsistencies reported here on the effects of crossbreeding on ovulation rate, along with the high

heritability estimates reported earlier, would tend to suggest that the genetic variation associated with ovulation rate is largely additive in nature.

Embryo Count, Weight and Survival Rate

To better understand how heterosis can increase productivity, several studies have been done to see how the embryo is affected by having parents of different breeds. In some earlier work with Chester White and Poland China gilts bred to boars of both breeds, virtually no difference was found in the number of embryos 25 days postbreeding (Robertson et al., 1951b). In contrast, Squires et al. (1952), working with inbred lines, found that cross line gilts lost 0.81 fewer embryos by the 25th day of gestation and 1.85 more embryos at that time when compared to the parental lines. This is similar to the findings of Reddy et al. (1958), who investigated differences among 56 purebred and 55 two-bred reciprocal cross gilts of outbred Landrace, Poland China and Duroc breeding. They found that crossbred gilts had 1.3 more embryos at 55 days of gestation than the corresponding purebreds, however this difference was not significant. In a study using purebred and two-breed cross gilts of Poland China and Chester White breeding, it was found that purebred fetuses, at 25 days of gestation, were significantly heavier than the crossbreds (552.5 vs 536.5 g, Baker et al., 1958). Seventy day purebred fetuses were still larger but not significantly so.

Johnson and Omtvedt (1973), evaluating 39 purebred and 80 two-breed cross litters from Yorkshire, Duroc and Hampshire dams, found that Duroc and Hampshire females carrying crossbred litters had a greater number of live embryos 30 days postbreeding (0.51 and 1.23, respectively) than did the purebreds, however this difference was not significant. Regardless of mating type, Yorkshire dams had similar numbers of embryos 30 days postbreeding. Two-breed cross litters were larger (0.64±0.52) than purebred litters 30 days into the gestation period. Survival rate, measured as percent live embryos of corpora lutea, was higher for the crossbred litters (5.44±3.83) than for the purebred litters, and average embryo length was similar for all mating types. From a later report of the same study, results from 212 gilts slaughtered 30 days postbreeding indicated that the level of crossbreeding of the dam and the litter may affect the relationship between the number of embryos at 30 days postbreeding and various reproductive traits (Young et al., 1974) It was also found that within each level of crossbreeding, purebred, two-breed cross and three-breed cross, the number of embryos in the litter at 30 days postbreeding was not significantly correlated with the size of the litter the dam was born in (-0.19, -0.10, -0.09, respectively). The number of purebred, two-breed cross and three-breed cross embryos was positively correlated with the ovulation rate of the dam, but the magnitude of these pooled

correlations were dissimilar (0.37, 0.24, 0.48, respectively). In a later report, Young et al. (1976) found positive but non-significant heterosis estimates for embryo count and embryo survival rate at 30 days of pregnancy. This analysis included 212 records of purebred gilts producing purebred and two-breed cross litters. Embryo survival rate (percent live embryos of corpora lutea) had an overall heterosis of 0.52±0.48, while embryo count at 30 days postbreeding had heterosis of 1.42±3.47. In a report originating in Canada, Dufour and Fahmy (1975) analyzed records of Landrace, Lacombe and Yorkshire females bred to Hampshire, Yorkshire and Landrace boars. Landrace sows with crossbred litters had 0.35 more embryos than did Landrace sows with purebred embryos. In contrast, Yorkshire sows with crossbred litters had 1.7 fewer embryos than did Yorkshire sows with purebred litters. Heterosis for weight of the fetuses was found to be 12, 5, and 4% for 23, 42 and 63 days of gestation, respectively.

Litter Size and Litter Weight at Birth

To properly evaluate how crossbreeding may affect the number born and litter weight at farrowing, it is necessary to first determine any difference between purebred and two-breed cross litters and then evaluate the difference between the purebred and crossbred dam farrowing crossbred litters. In this manner, purebred and crossbreeding systems can be evaluated properly.

Purebred vs. Two-breed Crosses

Many of the early experiments deal with the development of inbred lines and the response detected when those lines were crossed. It has been only during the last decade that there has been substantial interest in determining, experimentally, the effect of crossbreeding with modern breeds of swine.

In one of the first crossbreeding studies reported, two-breed cross litters of Yorkshire, Duroc, Chester White and Poland China breeding were 0.33 pigs per litter larger than purebred litters at birth (Winters et al., 1935). In trials using double-mated Duroc and Poland China sows, a lower percentage of crossbred stillborn pigs was observed and 2.5% heavier birth weights were recorded (Lush et al., 1939).

When investigating crosses among inbred lines, Chambers and Whatley (1951) found line cross litters were 0.48 pigs larger and 0.762 kg heavier at birth than inbred litters. In a study investigating reciprocal cross matings of six inbred lines formed from all possible crosses of Large Black, Poland China, Yorkshire, Duroc, Chester White and Landrace breeding, linecross litters were 1.2 pigs larger than inbred litters (Hetzer et al., 1961). Dickerson et al. (1959) analyzed data from stations involved in the Regional Swine Breeding Laboratory, and found that linecross litters

had an average superiority over the inbreds of 0.56 pigs at birth. In a review of combining ability studies involving inbred lines, litters which were the result of crossing two inbred lines showed increases in number born of 0 to 20% (Craft, 1953).

Results of 34,800 litters of Landrace and Large White breeding, in Great Britain, showed two-breed cross litters were 0.19 pigs larger at birth than purebred litters (Smith and King, 1964). O'Ferrall et al. (1968) developed crosses among inbred lines of Large Black, Chester White, Landrace, Duroc and Poland China swine. Crossbred litters (327 litters) were produced by mating inbred dams to a non-inbred boar of another breed while 229 inbred litters were produced. Linecross litters did not differ from inbred litters for number of pigs per litter at farrowing.

Duroc, Hampshire and Yorkshire purebred gilts and boars were mated to produce all possible two-breed cross and purebred litters, the crossbred litters were significantly larger (0.81 ± 0.36) and heavier (1.24 ± 0.38 kg) at birth than were purebred litters (Johnson and Omtvedt, 1973). In a later update of this study no significant difference remained for litter size and litter weight at birth between two-breed cross and purebred litters (Johnson and Omtvedt, 1975). Young et al. (1976) also found a non-significant difference for litter size at birth (0.38 ± 0.26) for Duroc, Yorkshire and Hampshire females giving birth to purebred and two-breed cross litters. However, an advantage of the two-

breed cross litters for litter weight at birth (0.50±0.27) did approach significance. In a summary of the studies reported above, two-breed cross litters sired by Duroc boars were 1.80±0.60 larger at birth than purebred litters. Litter weight at birth approached significance ($P<0.10$) for an advantage of 1.3±0.72 kg for crossbreds over purebreds. Two-breed cross litters sired by Hampshire boars were not different from purebred litters for litter birth weight and number born. Yorkshire boars sired two-breed cross litters that were significantly heavier at birth than purebred litters (1.4±0.62 kg) but were no different in the number of pigs farrowed (Johnson et al., 1978).

Gaugler (1980) used 366 purebred and crossbred litters (Duroc, Landrace, Spotted and Yorkshire) and found that two-breed cross litters were not significantly larger or heavier (0.09±0.40 and 0.26±0.24 kg, respectively). Kuhlers et al. (1980) used Landrace females mated with Landrace, Duroc and Yorkshire boars. The two-breed cross litters were then compared to the purebred Landrace litters. Crossbred litters were significantly larger than the Landrace litters for total number of pigs born (0.9). However, there was no difference in the number born alive. Two-breed cross litters did not differ significantly from the purebred litters for litter weight at birth. This is consistent with data from 137 purebred and 376 two-breed cross litters of Yorkshire, Hampshire, Duroc and Chester White breeding,

where heterosis for number born alive (-3.1%) and litter birth weight (2.3%) were not significant (Schneider et al., 1982).

Purebred vs. Crossbred Dams

To determine if crossbreeding is an effective tool for commercial breeding systems, comparisons must be made not only among purebred dams farrowing purebred and crossbred progeny, but also among purebred and crossbred dams that were mated to a boar of breeding unlike their own. Progeny from crossbred females that are mated to boars of similar breed composition do not exhibit the level of performance that is found with progeny that had sires of different breeding. These back cross progeny benefit from only half the heterosis that progeny with parents of different breeding have. However, the performance of back cross progeny has been less than expected in some studies (Winters et al., 1935; Winters, 1952; Rempel et al., 1964; Fahmy and Holtmann, 1977). Possible explanations of this are not clear cut. One explanation for this may be inadequate sampling in the trials reported. However, Dickerson (1969a) pointed out that recombination between genes from parental breeds could lead to modifications of epistatic deviations in the progeny and the heterosis measured might not be as large as expected. Another possibility may be that the decline in heterosis of the secondary crossbred population could be accounted for if the heterosis of the F_1 is due to

parental epistasis involving complementary genes, or if segregation has occurred in gene combinations that were additive in nature in the F_1 (Sheridan, 1981).

Winters et al. (1935), in one of the first studies comparing purebred and crossbred dams, found that two-breed cross dams farrowing three-breed cross litters (Yorkshire, Duroc, Chester White and Poland China) had 0.7 more pigs per litter than purebred dams farrowing two-breed cross litters. Lush et al. (1939) and Robison (1948) reported that crossbred females (Yorkshire, Duroc and Poland China) farrowing three-breed cross litters had 1.0 more pigs per litter than purebred, two-breed cross and backcross litters.

In a study of inbred and outbred Durocs, comparisons of three-line crosses to two-line crosses and outbred Duroc litters were reported. Two-line cross litters were significantly smaller and lighter (1.35 pigs and 1.33 kg) than three-line cross litters. Three-line cross litters were significantly larger (1.17 pigs) and heavier at birth (1.25 kg) when compared to outbred Duroc litters (Chambers and Whatley, 1951).

Bradford et al. (1953) used 3,841 purebred and crossbred litters (Spotted, Poland China, Duroc, and Chester White) from various Wisconsin farms, and found no advantage in litter size at birth when crossbred dams were compared to their purebred counterparts. This is similar to results reported from 315 purebred, two-breed, three-breed and four-

breed cross litters of Poland China, Landrace, Hampshire and Duroc breeding (Smith and McLaren, 1967). Little difference was indicated between two- and three-breed cross litters for number at birth, however three-breed cross litters were somewhat heavier at birth. This conflicts with the findings of Gaines and Hazel (1957), who found that crossbred sows had a significant advantage over purebred sows for number born at farrowing. They also showed that Duroc x Poland China x Landrace sows farrowed more pigs when bred to a fourth breed of boar than when using one of the parental breeds.

Duroc, Hampshire and Yorkshire swine were mated to produce 835 purebred, two-breed cross and three-breed cross litters (Johnson et al., 1978). Two-breed cross females farrowed litters that had 0.93 ± 0.32 more pigs and were 1.0 ± 0.39 kg heavier at birth than purebreds. In a study where Duroc x Landrace and Yorkshire x Landrace dams were compared to purebred Landrace sows, 305 litters sired by Duroc, Spotted or Hampshire boars were produced (Kuhlers et al., 1981). Crossbred sows had litters that were similar in number at farrowing to Landrace sows farrowing two-breed cross litters. Crossbred dams did produce litters that were heavier (1.45 kg) than the litters produced by Landrace dams.

Schneider et al. (1982) summarized 1,065 purebred, two-breed cross, paternal back cross and maternal back cross litters of Chester White, Duroc, Hampshire and Yorkshire

breeding. Crossbred dams had litters which had 0.95±0.36 more pigs and were 1.46±0.47 kg heavier at birth when compared to purebred dams.

Heritability and Correlation Estimates of Boar Testicular Traits

A summary of reported heritability estimates of testicular traits can be found in Table XI. The reported heritability estimates for epididymidal weight and testicular weight suggest that these traits are moderately to highly heritable. Phenotypic correlations among testicular traits have been reported in several studies, however inconsistency among traits measured makes interpretation difficult. Testis weight was found to be moderately correlated with testicular sperm count (Wilson et al., 1977, r=0.65; Courot and Legault, 1979, r=0.59; Fent, 1980, r=0.50). Wilson et al. (1977) and Fent (1980) reported moderate correlations (0.49 to 0.66) among cauda epididymidal weight, number of caput-corpus epididymidal sperm and number of caput-corpus epididymidal sperm with testicular weight. Davis and Hines (1977) reported that in boars that averaged 117.03 kg, excised testes length and width were highly associated with testes weight (r=0.84). This agrees with the findings of Schinkel (1980), who reported a correlation of 0.81 for both length and width of testes, measured *in situ*, with testicular weight in 90.7 kg boars. Epididymidal weight was found to be moderately

associated with *in situ* testes length and width in 90.7 kg boars (r=0.61).

TABLE XI

SUMMARY OF HERITABILITY ESTIMATES FOR BOAR TESTICULAR TRAITS

Author	N_P	N_L	N_S	Breed or Line	Method	Trait	h^2	SE
Courot and Legault, 1977	95	53	8	LW		TWT	.34	.33
						TTS	.42	.37
						TEPW	.38	.35
						TEPS	.42	.37
Legault et al., 1979	226		16	LW		TEPW	.35	
						TWT	.73	
						TWT+TEPW	.77	
				Weighted average		TWT	.61	(2)[1]
						TEPW	.36	(2)

[1]Number in parentheses indicates the number of estimates in the weighted average.

When boars were measured at young constant ages, *in situ* measurements of testes length and width were lowly associated with testes and epididymidal weight (ages ranged from 120 to 183 days, correlations ranged from -0.02 to 0.32). In contrast to this, boars that were 42 days older showed moderate to high correlation of testes and

epididymidal weights to length and width of testes measured *in situ* (correlations ranged from 0.71 to 0.83).

Cauda epididymidal weight has been found to be lowly to moderately associated with number of testicular sperm (Wilson et al., 1977, r=0.28; Fent, 1980, r=0.28). While number of caput-corpus and cauda epididymidal sperm has been found to be moderately to highly associated with cauda epididymidal weight, with estimates ranging from 0.34 to 0.71 (Wilson et al., 1977; Fent, 1980). These studies reported a phenotypic correlation of 0.45 for number of testicular sperm with number of cauda epididymidal sperm. This was similar to their reports for phenotypic correlations of number of caput-corpus epididymidal sperm with cauda epididymidal sperm (Wilson et al., 1977, r=0.47; Fent, 1980, r=0.50). Phenotypic correlations for number of cauda epididymidal sperm with testicular sperm count ranged from 0.40 to 0.51.

Effects of Crossbreeding on Boar Reproductive Traits

The effects of crossbreeding for reproductive and maternal traits have been well documented for the crossbred female. There has been limited and somewhat scattered documentation of how crossbred males compare to purebred males. This can possibly be attributed to industry tradition and the popular, but undocumented, belief that

crossbred sires would produce progeny that would be more variable in their performance than those of purebred sires. Limited published reports have not supported this belief. Many of these reports have indicated that crossbred boars reach sexual maturity at a younger age than do purebreds. This suggests that crossbred boars could play a successful role in commercial swine production.

Testicular Traits

In one of the earlier studies investigating how crossbreeding may affect a sire's performance, Hauser et al. (1952) crossed inbred lines of Poland Chinas, Hampshires and outbred Durocs and compared them to the purebred groups. Crossbred boars exhibited average heterosis estimates of 30% and 27% for testes and epididymidal weight, respectively. Crossline boars demonstrated heterosis of 20% for stage of spermatogenesis.

Wilson et al. (1977) studied purebred and crossbred boars of Duroc and Hampshire breeding and found that at 7.5 to 9 months of age crossbred boars had 16% heavier testes weights and 25.1% more testicular sperm than did purebreds. Crossbred boars had more caput-corpus epididymidal sperm ($5.28 \pm 4.3 \times 10^9$) and cauda epididymidal sperm ($12.36 \pm 8.73 \times 10^9$) than did purebred boars, but these differences were not significant. Purebred boars, however, did have significantly lighter cauda epididymides (6.74 ± 3.29 g) than crossbreds.

Conlon and Kennedy (1978) compared crossbred Hampshire x Duroc boars to purebred Hampshire, Duroc and Landrace boars. Heterosis for semen volume in the Duroc x Hampshire crosses was 229.2%, but the crossbred boars were no better than the purebred Landrace. Hampshire x Duroc boars demonstrated an 11.4% higher sperm morphology score, but had the lowest score for live-dead rate.

Neely et al. (1980) investigated testicular and seminal traits of purebred and crossbred boars (Yorkshire and Duroc) at 56, 84, 112, 140 and 168 days of age. With the exception of testes length at 84 and 112 days and testes width at 84 days, crossbred boars had longer and wider testes than did purebred boars, with heterosis values ranging from 5.7 to 9.5%. Boars were castrated between 160 and 175 days of age and crossbred boars had 25.4% heavier testes. Heterosis values for total number of sperm and sperm per gram of testis were 33.7 and 23.7%, respectively. Corpus epididymidal weight was significantly heavier and cauda epididymidal weight was more in crossbred boars, but not significantly so. There were no significant breed group differences for caput epididymidal weight and caput, corpus and cauda sperm numbers.

Fent (1980) collected testicular, seminal and plasma hormone data on approximately 120 crossbred and purebred boars of Spot, Duroc, Landrace and Yorkshire breeding. Blood samples were taken immediately before gonadotropin

releasing hormone injection. Blood samples were then taken at hourly intervals for four hours. Boars were castrated after sampling. Crossbred boars had heavier testes, caput-corpus epididymides and cauda epididymides than purebred boars. Total sperm numbers for the testes and the two epididymidal segments were larger in the crossbreds. Crossbred and purebred boars had similar levels of plasma luteinizing hormone, except at three and four hours after gonadotropin releasing hormone administration, and serum testosterone levels in purebred and crossbreds were similar at four hours after treatment.

Mating Behavior

Unfortunately, mating behavior studies are not frequently performed. The subjectivity of the data collection can lead to biases that cannot be accurately measured. However, this type of data is important to properly evaluate what differences may exist between crossbred and purebred sires.

Wilson et al. (1977) reported that 28 of 36 crossbred boars mated every time when exposed to an estrus gilt. Only 11 of the 36 purebred boars mated every time. No crossbred boar had more than one failure to mate, while 42% of the purebred boars had two or more failures. However, no significant difference existed between breed groups for the interval from exposure to an estrus gilt to ejaculation time.

The mating behavior of reciprocal Duroc-Yorkshire crossbreds was compared to purebred Duroc and Yorkshire boars of similar age (8 to 10 months) (Neely and Robison, 1983). Sexual interest was scored on a scale of 0 to 2 (0=no sexual interest, 2=strong interest), and crossbreds exhibited more sexual interest (51.7% heterosis), had a higher percentage of proper mounts (1.9% heterosis) and more total mounts (31.7% heterosis). Crossbred boars also had the shortest time to first proper mount, to final mount and to completion of successful mating (heterosis of -34.2, -28.6 and -20%, respectively).

Reproduction Efficiency

Reproductive efficiency of a sire is a measure of conception rate and number of embryos or pigs born per dam exposed. Wilson et al. (1977) measured reproductive efficiency on 195 Duroc, Hampshire and reciprocal cross boars. No breed group differences in reproductive efficiency were significant. Crossbred boars settled 7.9% more gilts, but this can be partially attributed to Hampshire boars settling 14.6% less than Durocs. Crossbred boars sired 1.11±0.94 more embryos per gilt exposed and sired litters that had 0.59±0.65 more embryos at 30 days of gestation than did purebreds. These findings were similar to those of Conlon and Kennedy (1978), who found that crossbred Hampshire x Duroc boars did not have a

significantly higher conception rate (1.6% heterosis) than purebred Hampshire and Duroc boars.

Buchanan and Johnson (1983) conducted analyses on 161 purebred and two-breed cross boars of Duroc, Landrace, Spotted and Yorkshire breeding that were used to produce three- and four-breed cross litters. Crossbred boars had a 17.9% higher first service conception rate, but only a 5.3% higher 8-week breeding season conception rate than did purebred sires. They did require 0.11 fewer services per conception than did purebred boars. Differences for litter size and litter weight at birth among litters sired by crossbred and purebred boars were small.

It would appear that reproductive traits, with a few exceptions, are lowly to moderately heritable in both sexes. Reported correlations among reproductive traits within each sex are inconsistent, which may be due to the relatively small numbers used in many of the studies. Reproductive traits do appear to respond favorably to crossbreeding in both the boar and the gilt.

Reproduction Traits in the Bull

The development of artificial insemination techniques in cattle has caused greater study of male reproductive traits in the bull than in the boar. However, many of the traits reported for the bull are not applicable to the boar. Table XII contains a listing of reported heritability estimates for semen traits. The range of these estimates is

TABLE XII

SUMMARY OF HERITABILTY ESTIMATES FOR SEMEN TRAITS IN BULLS

Author	N_P	N_S	Trait	Breed	Method	h^2	SE
Brinks et al., 1973	435		Semen Concentration	Hereford	PHS	.28	.116
Silva et al., 1980		12	Semen Concentration	Gir and Nellore		.25	
Knights, 1983	717	80	Semen Concentration	Angus	PHS	-.13	.06
Brinks et al., 1973	794		Percent Live Sperm	Hereford		.17	
Silva et al., 1980		12	Percent Live Sperm	Gir and Nellore		.40	
Knights, 1983	717	80	Percent Live Sperm	Angus	PHS	0	
Neely et al., 1982	578	66	Sperm per Gram of Testis	Hereford	PHS	-1.3	.18
			Total Sperm in Testis			.14	.21
			Right Testis Weight			.63	.27
			Scrotal Length, 205[a]			.07	.20

TABLE XII (Continued)

Author	N_P	N_S	Trait	Breed	Method	h^2	SE
			Scrotal Dia., 365[a]			.28	.24
			Scrotal Length, 365[a]			.16	.21
			Scrotal Dia., 365			.40	.24
			Excised Testes, Length			.19	.26
			Excised Testes, Width			.02	.24

[a]205 = 205 days of age; 365 = 365 days of age.

-1.3 to 0.63. This suggests that semen traits are lowly to moderately heritable. A listing of reported heritability estimates for scrotal circumference can be found in Table XIII. The weighted average heritability estimate is 0.55.

Knights (1983), summarizing several studies, reported a weighted average phenotypic correlation of 0.72 for testis weight and sperm number produced. Sperm concentration and percent live cells was reported to have a phenotypic correlation of 0.048 and a genetic correlation of 0.259 ± 0.47 (Abadia et al., 1973). Johnson et al. (1974) found total testes sperm to be highly correlated with testes weight (0.73) and sperm per gram of testis (0.91) in yearling Hereford bulls.

In a study of 578 Hereford bulls, scrotal circumference at one year of age was found to have phenotypic correlations of 0.87, 0.63 and 0.16 with excised testes circumference, total sperm in testes, and sperm per gram of testis, respectively (Neely et al., 1982). Excised testes circumference was found to be moderately correlated with total sperm in testes (0.54) and sperm per gram of testis (0.33). Scrotal length at a year of age was found to have correlations of 0.77, 0.54 and 0.33 with excised testes length, total sperm in testes and sperm per gram of testis, respectively. Genetic correlations were not significant and ranged from 0.06 to 1.3.

TABLE XIII

SUMMARY OF HERITABILITY ESTIMATES FOR SCROTAL CIRCUMFERENCE OF BULLS

Author	N_P	N_S	Breed	Age	Method	h^2	SE
Coulter et al., 1976	389	70	Holstein	6-72 months	PHS	.67	.10
	319	52	Holstein	6-11 months	PHS	.62	.09
	642	81	Holstein	12-17 months	PHS	.78	.07
Blockey et al., 1978	438		Hereford	16-22 months	PHS	.59	.16
	331		Angus				
Coulter and Keller, 1979	1984		Beef			.69	.15
Latimer et al., 1982	569	117	Angus	225 days	PHS	.60	.17
	569	121	Angus	365 days	PHS	.38	.16
Neely et al., 1982	578	66	Hereford	205 days	PHS	.08	.20
	578	66	Hereford	365 days	PHS	.44	.24
Knights, 1983	717	80	Angus	365 days	PHS	.36	.06
				Weighted average		(.55)	(10)[a]

[a]Number of estimates used in estimating the weighted average.

Relationships Among Female and Male Sex-Limited Traits

Many of the economically important traits are often sex-limited traits. It is difficult to make rapid improvement in these traits, since selection is limited to the sex for which the trait is expressed. The dairy industry has dealt with this problem with extensive progeny testing to determine which bulls sire higher milk producing females. Progeny testing is time consuming and costly, and can be feasibly only through intensive marketing procedures. For these reasons this procedure has limited potential in other livestock species.

Reproductive efficiency is the most important trait to the commercial producer. If programs were available to allow for greater response to selection for reproductive efficiency, greater profits could be realized. It has been suggested that

> . . . the expression of reproductive activity in males and females shows that it, itself, is not sex-limited. It is the expression of reproductive activity which is influenced by the sex of the individual (Land, 1978, p. 52).

Reproductive function in both males and females is controlled by the same hormones. Also, with the exception of the Y chromosome, the genotypes of males and females do not differ. If reproductive traits in both sexes are being controlled by the same gene pairs and those traits are identified, then selection intensity could be increased and

thus greater improvement of those traits of interest could be achieved. However, this is not easily done. Pleiotropic effects of a gene pair or gene pairs may not be of the same degree in one sex as it is in the other. Traits that are genetically related may not have the same number of gene pairs controlling each trait. Also, the relationship between gene pairs on somatic chromosomes with those on sex chromosomes is not fully understood. These plus many other possibilities make determination, of traits that are of the same genetic control in different sexes, difficult. However, there is an increasing amount of work that has been done to try and find a solution to this problem. The following is a review of studies involving sheep, mice, cattle and pigs, which have tried to determine the relationship that may exist between traits peculiar to different sexes.

Sheep

In a study comparing reproductive traits of two breeds, Finnish Landrace rams were found to have larger testes diameter than did Tasmanian Merinos. Testes diameter was also found to be positively related to ovulation rate within each breed (Land, 1973). It has been shown that differences in luteinizing hormone activity may be related to differences in sheep fertility (Land et al., 1972; Thimonier et al., 1972). Follicle stimulating hormone and luteinizing hormone control the development of follicles and ovulation

in females and also spermatogenesis and testosterone production in males. It is then possible that the inheritance of the action of these hormones is the same in both sexes.

It has been reported that gonadotrophic stimulation rather than inherited growth potential has greater control of testis development (Land and Carr, 1975). When Finnish Landrace, Blackface and Merino ram lambs were hemicastrated, the hypertrophy of the remaining testis was inversely related to the ovulation rate of the breed. The variation in testes growth could be caused by breed differences to negative feedback to the testes. Even though monitoring hormone levels may not be a practical selection tool, the feedback control of gonadotrophin may be controlled by the same gene pairs in both sexes and could explain the association between different components of reproduction (Land, 1978). With this argument in mind, female reproductive performance may be increased by selection for increased testes size.

Mice

Land (1973), working with mice that have been selected for ovulation rate for 12 generations, found that the correlation between mean testis weight and mean ovulation rate was 0.97. After changes in body weight were accounted for, the partial correlation between ovulation rate and

testes weight was 0.82. In a study where testis weight was selected for, for five generations, testis weight was found to have a genetic correlation of 0.50±0.18 with ovulation rate in primiparous females and 0.25±0.20 with ovulation rate in nulliparous females (Islam et al., 1976). In an experiment where lines of mice were selected for large and small liter size, Joakimsen and Baker (1977) found highly significantly differences between lines for testes weight. Lines selected for increased litter size resulted in males of these lines having heavier testes weights. It would appear that in mice, testes weight is positively related to litter size.

Cattle

It has been determined that scrotal circumference in bulls is a moderately to highly heritable trait (Table XIII). Since this is a reasonably easy trait to measure, it would be advantageous if this trait were optimally related to reproductive traits in the female. Selection pressure could then be applied to both sexes with minimum difficulty.

In Hereford, Red Angus and Angus cattle, age at puberty in heifers was found to have a genetic relationship of -0.71 with the scrotal circumference of their half-sib brothers. Age at puberty was also found to be genetically correlated with percent normal sperm (-0.37) and motility (0.33) (Brinks et al., 1978). Reports from the MARC breed analysis study indicate that beef breeds that have bulls with larger

testes will have heifers that reach puberty at a younger age (Lunstra, 1982). Knights (1983) reported that estimates of genetic correlations were outside the parameter space for scrotal circumference and maternal traits (MPPA for birth and weaning weight and age at first calving). However, the covariance was favorable for scrotal circumference and age at first calving. The genetic correlations of scrotal circumference with milk and fat production were -0.19 ± 0.12 and -0.12 ± 0.12, respectively (Coulter et al., 1977). The corresponding genetic correlations for testicular consistency were -0.08 ± 0.09 and -0.05 ± 0.09.

Swine

Studies investigating the relationship between male and female reproductive traits are limited in number. Schinckel (1980) reported low to moderate phenotypic correlations for testicular traits with age at puberty and ovulation rate in full sisters. The phenotypic correlation between a gilt's age at puberty and ovulation rate with her subsequent son's testicular traits were smaller in magnitude. The genetic correlation of testis weight with ovulation rate ranged between 0.39 and 0.65, if the heritability of testis weight is between 0.3 and 0.6.

It would appear that the relationship between gonadal traits (e.g., testis weight and ovulation rate) of different sexes is favorable. This may be due to the similarities of

the physiological mechanisms involved in the control of these organs. The relationship, if one exists, between testicular traits and maternal traits is not yet clear. The benefit of finding favorable relationships between reproductive traits of both sexes would allow for faster genetic progress. However, selection programs should not abandon their present status until more results are obtained. The magnitude of these relationships between reproductive traits of different sexes is not yet understood, thus the consequence of selection cannot yet be predicted accurately.

CHAPTER III

MATERIAL AND METHODS

Experimental Design

Purebred and two-breed cross litters were produced in a four breed diallel mating system utilizing the Duroc, Yorkshire, Spotted and Landrace breeds of swine. Pigs were produced for five consecutive seasons beginning in the fall of 1976 at the Stillwater Swine Research Farm. Reproductive traits for littermate boars and gilts were evaluated.

Spot and Landrace herds were formed at the farm in the spring of 1976. Twenty-five gilts and four boars of Landrace and Spot breeding were purchased so that 20 litters per season per breed would be produced. Landrace gilts were purchased from nine different sources. These gilts were primarily of American Landrace ancestry. Two Swedish and two Canadian Landrace boars were obtained from four different breeders. Spot gilts and boars came from nine different herds. Yorkshire and Duroc herds of a broad genetic base had been maintained in Stillwater for several years. This was accomplished primarily by purchasing test station boars from several states.

To maintain a broad genetic base in all four herds, one

or more boars of each breed were replaced each season. Duroc and Spot boars were selected for post-weaning growth, backfat and feed efficiency when appropriate. These traits were combined in a selection index approved for boar test stations by the Swine Improvement Federation (Hubbard, 1981). Yorkshire and Landrace boars were selected on the number of pigs and the weight of the litter in which they were weaned. Replacement gilts were selected within herds, based primarily upon an index of growth and backfat.

Husbandry

Litters were farrowed twice yearly, with spring litters born in March and April and fall litters born during September and October. Females were hand-mated during an eight week breeding season and were fed 1.8 to 2.2 kg of a 15 percent crude protein, sorghum grain or corn based ration in pastures. Sows were farrowed in a central confinement farrowing facility and were moved at 7 to 14 days post-farrowing to an open-front confinement building with one litter per pen, or to pasture lots with three or four litters per lot. Litters were weaned at 42 days of age, with the two heaviest males left intact. At eight weeks of age, pigs were assigned to growing-finishing facilities for gain test.

Boars were allotted to open front confinement pens by breed group with ten boars per pen. All boars were allowed to consume a 14% crude protein, corn or sorghum grain and

soybean meal ration ad libitum. At 100 kg, boars were removed from test and probed for backfat thickness. Five boars of each purebred and crossbred group were then randomly chosen to be transferred to the Southwestern Livestock and Forage Research Station (SLFRS), El Reno, Oklahoma, to be used as breeding animals. Only one boar per litter was selected. Testicular, seminal, and hormonal characteristics were evaluated in a full-sib brother of each boar sent to the SLFRS.

Gilts were randomly selected within breed groups to be raised in either pasture lots with barrows or confinement pens, ten gilts per pen. Confinement pens of gilts were arranged such that all gilts were exposed to boars of similar age (at least one adjacent pen), except in the fall of 1976 when only half the gilt pens were adjacent to boars.

Gilts in confinement pens and pasture lots were allowed to consume a 14 percent crude protein, sorghum grain or corn based ration ad libitum during the test period. Gilts were weighed weekly until reaching 90.7 kg, when they were removed from gain test and probed for backfat. Gilts were then transported to the SLFRS and put into pasture lots. They were fed 1.8 to 2.2 kg of a 15 percent crude protein ration per day. Estrus detection was accomplished in these pasture lots by placing a teaser boar in with the gilts daily. Teaser boars were kept in the pens for 15 to 20 minutes, with no more than 30 head per pen, to provide

uniform stimulation. As littermate boars of these gilts started to exhibit libido, these animals were then used for estrus detection purposes.

Data Collection

The ages and weights at puberty of gilts were available. Age and weight at puberty were defined as the actual age and weight when gilts attained first detected estrus as indicated by a standing response to a teaser boar. Any gilt which was lame, showed signs of disease or died before reaching 219 days of age was omitted from the data.

Full-sib brothers were left intact and retained for study. Boars that remained in Stillwater were transferred from the Swine Research Farm to the Nutrition-Physiology Research Center (NPRC), at approximately seven months of age. While at the NPRC boars were fed 2 kg per day of a 14 percent crude protein ration.

Blood samples were taken to evaluate plasma luteinizing hormone (LH) and testosterone during every season. Twenty-five milliliter blood samples were taken, prior to an intramuscular injection of gonadotropin releasing hormone (GnRH:Abbott Laboratories) and at 1, 2, 3 and 4 hours after GnRH treatment, from each boar. For all seasons except for the spring of 1978, boars were castrated one day after blood sampling. The right testis was retained and total sperm number and weight of testes, caput corpus and cauda epididymides were measured. Detailed protocol of the blood

sampling analysis and sperm number quantification was documented by Fent (1980).

Purebred and two-breed cross boars which were transferred to the SLFRS were approximately eight months of age at the beginning of each eight week breeding season. During the five seasons boars were mated to two-breed females of breeds other than their own, to produce all possible three-breed (purebred sires) and four-breed (crossbred sires) cross litters. For the first season, boars were mated to gilts only, however during the four subsequent seasons a random sample of sows were retained for breeding. Through the time of the eight week breeding season, estrus detection was accomplished by the use of a teaser boar. Females were brought to dirt floored pens to be hand mated. Matings were recorded and if a female returned to estrus she was bred to the boar used in the previous mating. A service was defined as the exposure of a gilt to a boar during an estrus period. The average number of services per conception was recorded for each sire. The percentage of females settled of females exposed (average conception rate) was calculated for each sire.

Statistical Analysis

Models used in computation of variance and covariance components for heritability and correlation estimation were adapted from authors who had previously reported analyses of

these data (Fent, 1980; Buchanan and Johnson, 1983). The model used for testicular or epididymidal characteristic is as follows:

$$Y_{ijklm} = u+D_i+L_j+S_k+M(D)_{li}+DL_{ij}+e_{ijkl}$$

For hormone or breeding performance of boars the following model was used:

$$Z_{ijklm} = u+D_i+L_j+S_k+M(D)_{li}+DL_{ij}+DS_{ij}+LS_{jk}+DLS_{ijk}+e_{ijklm}$$

The terms in these models were:

Y_{ijklm} = observation of the m^{th} testicular or epididymidal characteristics of a boar sired by the l^{th} sire of the i^{th} sire breed, born in the k^{th} season to the j^{th} breed of dam;

Z_{ijklm} = observation of the m^{th} serum hormone level or breeding performance record of a boar sired by the l^{th} sire of the i^{th} sire breed born in the k^{th} season to the j^{th} breed of dam;

u = population mean;

D_i = fixed effect of the i^{th} breed of sire, i = 1,2,3,4.

L_i = fixed effect of the j^{th} breed of dam, j = 1,2,3,4;

S_k = fixed effect of the k^{th} farrowing season, k = 1,2,3,4 (testicular and epididymidal data); k = 1,2,3,4,5 (plasma hormone data and breeding performance records);

$M(D)_{li}$ = random effect of the l^{th} sire within the i^{th} sire breed;

DL_{ij} = interaction between the i^{th} breed of sire and the j^{th} breed of dam;

DS_{ik} = interaction between the i^{th} breed of sire and the k^{th} farrowing season;

LS_{jk} = interaction between the j^{th} breed of dam and the k^{th} farrowing season;

DLS_{ijk} = interaction of the i^{th} breed of sire, the j^{th} breed of dam and the k^{th} farrowing season;

e_{ijklm} = random error associated with the $ijklm^{th}$ observation.

The breed of sire by breed of dam by farrowing season interaction was included because Fent (1980) found it to be significant for serum testosterone levels at three and four hours after GnRH injection, but not for testicular or epididymidal. The model for the breeding performance traits was the same as was used for the serum hormone levels.

Variance Component Estimation

Sire within breed of sire and residual variance and covariance components were estimated for the following individual boar traits: testicular weight, caput-corpus epididymidal weight, cauda epididymidal weight, testicular sperm number, caput-corpus epididymidal sperm number, cauda epididymidal sperm number, total epididymidal weight, total epididymidal sperm number, number of sperm per gram of testis, basal levels of plasma LH and testosterone, hourly levels of plasma LH and testosterone after GnRH injection for four hours, average number of services per conception, and average conception rate. Variance and covariance components were estimated using Method III (Henderson, 1953).

Heritability Estimation

Paternal half-sib heritability estimates were calculated using the formula:

$$h^2_Y = \frac{4Vs}{Vs+Ve}$$

where:

h^2_Y = heritability estimate of trait Y;

Vs = sire variance component estimate for trait Y;

Ve = residual variance component estimate for trait Y;

Standard errors for heritability estimates were calculated using an approximation formula reported by Swiger et al. (1964):

$$V(h^2) = 16\ \frac{2(N-1)(1-t)^2+[1+(k-1)t]^2}{k(N-s)(s-1)}$$

where:

K = sire variance component coefficient from the expected mean square;

$t = \frac{Vs}{Vs+Ve}$;

N-1 = corrected total degrees of freedom;

N-s = error degrees of freedom;

s-1 = sire degrees of freedom.

Vesely and Robison (1970) discussed in their paper that this approximation formula does not take into account adjustments made for fixed effects and as such yields minimum estimates for these standard error estimates.

Genetic Correlation Estimates

Genetic correlations of traits can be divided into two different categories: 1. correlations between two traits expressed in an individual, and 2. correlations between traits expressed in different individuals within a litter. In this study, correlations among traits expressed in the same individual were calculated by estimating the sire variance and covariance components as discussed by Falconer (1981). The formula for this is as follows:

$$r_g = \frac{Cxy}{\sqrt{V(X)\ V(Y)}}$$

where:

Cxy = component of covariance between sire estimates for trait x and trait y;

V(X) = estimate of the sire variance component for trait x;

V(Y) = estimate of the sire variance component for trait y.

In his discussion, Falconer explains that the Cxy component has an expectation of one-quarter of the covariance of the breeding values of the two characters. When dividing by the square root of the product of the sire variance components for the two traits, the expectation of r_g becomes:

$$r_g = \frac{C_A}{AX\ \ AY}$$

where:

C_A = covariance component among the additive gene effects for trait X and Y;

AX = standard deviation for the additive gene effects for trait X;

AY = standard deviation for the additive gene effects for trait Y.

Standard errors were calculated using an approximation formula described by Dickerson (1969b). The formula is as follows:

$$V(r_g) = r_{gxy}\left[\frac{V(\hat{\sigma}_{xy})}{\sigma_{xy}^2} + \frac{V\hat{\sigma}_x^2}{4(\hat{\sigma}_x^2)^2} + \frac{V\hat{\sigma}_y^2}{4(\hat{\sigma}_y^2)^2} - \frac{C\,\hat{\sigma}_{xy}\hat{\sigma}_x^2}{\hat{\sigma}_{xy}\hat{\sigma}_x^2} - \frac{C\,\hat{\sigma}_{xy}\hat{\sigma}_y^2}{\hat{\sigma}_{xy}\hat{\sigma}_y^2} + \frac{C\hat{\sigma}_x^2\hat{\sigma}_y^2}{2\hat{\sigma}_x^2\hat{\sigma}_y^2}\right]$$

where:

$V(r_g)$ = the variance of the intraclass genetic correlation estimate;

r_{gxy} = intraclass genetic correlation estimate;

$V\hat{\sigma}_{xy}$ = estimated variance component for the sire covariance component estimate for traits X and Y;

$\hat{\sigma}_{xy}^2$ = square of the sire covariance component estimate for traits X and Y;

$V\hat{\sigma}_x^2$ = estimated variance component for the estimated sire variance for trait X;

$V\hat{\sigma}_y^2$ = estimated variance component for the estimated sire variance for trait Y;

$\hat{\sigma}_x^2$ = estimated sire variance component for trait X;

$\hat{\sigma}_y^2$ = estimated sire variance component for trait Y;

$C\,\hat{\sigma}_{xy}\hat{\sigma}_x^2$ = estimated covariance component between the sire covariance component for traits X and Y and the sire variance component for trait X;

$\hat{\sigma}_{xy}$ = estimated sire covariance component for traits X and Y;

$C\hat{\sigma}_{xy}\hat{\sigma}^2_y$ = estimated covariance component between the estimated sire covariance component for traits X and Y and the sire variance component for trait Y;

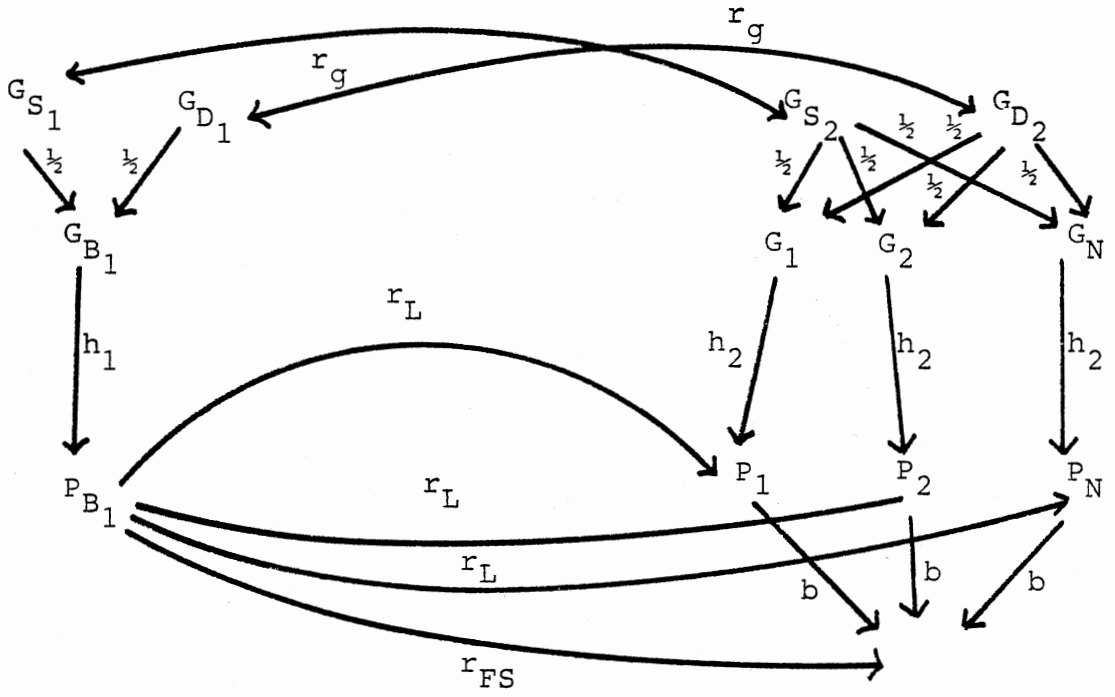
$C\hat{\sigma}^2_x\hat{\sigma}^2_y$ = estimated covariance component for the estimated sire variance components for traits X and Y.

Another purpose of this study was to determine the correlation between a boar's reproductive and breeding performance traits and his littermates' reproductive performance. During four of the five seasons of this study, boars that were left intact for breeding purposes or for study of reproductive organs had littermate sisters that were evaluated for age and weight at puberty. Boars that had been left intact for later blood sampling and castration had full brothers that were a part of the breeding herd for all five seasons of the study. This allowed study of the relationships between a boar's testicular data and endocrine profile and his littermate sister's age and weight at puberty records, a boar's breeding performance and his littermate's age and weight at puberty records, and a boar's breeding performance and his brother's testes characteristics and endocrine profile.

Pooled, within class, correlations were calculated for a boar's testicular data and hormone profile with age and weight at puberty of his littermate sisters. For the testicular and epididymidal traits, 73 boars had sisters represented in the data set, while 90 boars which had

hormone data collected had sisters with age and weight at puberty records. Means of the full-sib sisters were used to calculate the correlation coefficients with the boar traits for those litters that had more than one chosen gilt. This increased the estimate of the correlation when compared to those expected if individual observations of the female traits had been used. The increase is the product of N and b, where N is the harmonic mean of the number of full-sibs in each family mean and b is the standard partial regression coefficient of the phenotypic mean of a family on an individual observation. This leads to the formula $r_{FS} = 1/2h_1h_2r_gN_b$ from which an approximation of the genetic correlation can be found by solving the equation. This was developed by methods discussed by Schinckel (1980) and is illustrated in Figure 1. The harmonic mean for the number of full-sibs that had brothers being castrated was 2.194 while the harmonic mean for full-sibs with brothers with hormone data was 2.284.

Figure 1 also illustrates the relationship between a boar's breeding performance and the average of his littermate sister's age and weight at puberty. Breeding performance traits were average number of services per conception and average conception rate. Average number of services per conception is defined as the mean number of exposures to an estrus female per recorded pregnancy during an eight week breeding season. Average conception rate is



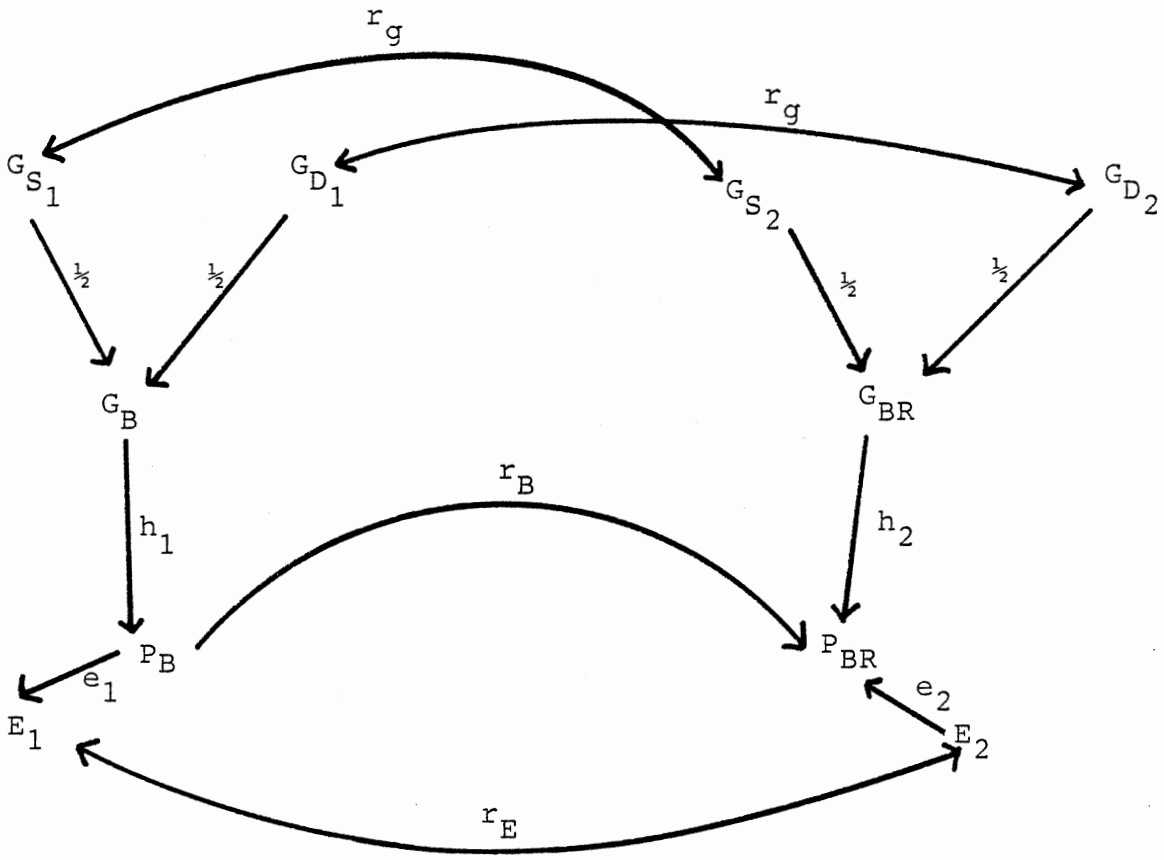
$$b = \sqrt{\frac{1}{\frac{N+N(N-1)}{2}\ h_2}}$$

b = standard partial regression coefficient of the phenotypic mean of a family on an individual observation;
N = harmonic mean of the number of full sibs in each family mean;
r_L = phenotypic correlation between male trait 1 and trait 2 expressed in a full-sib;
r_{FS} = phenotypic correlation between male trait 1 and the average of the male's full-sib sisters for trait 2;
r_g = genetic correlation between male trait 1 and trait 2 expressed in his full-sib;
P_1-P_N = phenotypic value of the full-sibs for trait 2;
P_B = phenotypic value of the boar for trait 1;
P_{FS} = average phenotypic value of the full sibs for trait 2;
G_1-G_N = genotypic values of the full sibs for trait 2;
G_{B1} = genotypic value of the boar for trait 1;
G_{S1} = genotypic value of the sire for trait 1;
G_{S2} = genotypic value of the sire for trait 2;
G_{D1} = genotypic value of the dam for trait 1;
G_{D2} = genotypic value of the dam for trait 2.

Figure 1. Path Coefficient Diagram Relating a Boar's Performance for a Male Trait with the Mean Performance of His Littermate Sister's Performance for a Female Trait

the number of exposures to an estrus female during an eight week breeding season divided by the number of recorded pregnant females. There were 108 boars with breeding performance records that had full-sib sisters with age and weight at puberty data recorded. Pooled, within class, correlations of average number of services per conception and average conception rate with full sib means for age and weight at puberty were calculated. Consequences of this method of computation are as discussed earlier. The harmonic mean for the number of full-sibs with brothers with breeding performance records is 2.287.

Pooled, within class, correlation coefficients were calculated for a boar's breeding performance and his littermate brother's testicular and hormone data. There were 78 boars with testicular data that had brothers with breeding performance data and 91 boars with hormone data that had brothers with breeding performance records. The equation to calculate the approximation of the genetic correlation is $r_{pb} = 1/2h_1h_2r_g + e_1r_ee_2$. For these analyses it was assumed that the correlation between environments (r_e) is zero. This allows the solution for the genetic correlation to be $r_g = 2r_B/h_1h_2$. This is illustrated in Figure 2.



r_E = correlation between environment 1 and environment 2;
r_B = phenotypic correlation between male trait 1 and trait 2 expressed in the full sib;
r_g = genetic correlation between male trait 1 and that trait expressed in the full sib;
P_B = phenotypic value of the boar for trait 1;
P_{BR} = phenotypic value of the full sib for trait 2;
G_B = genotypic value of the boar for trait 1;
G_{BR} = genotypic value of the full sib for trait 2;
G_{S_1} = genotypic value of the sire for trait 1;
G_{S_2} = genotypic value of the sire for trait 2;
G_{D_1} = genotypic value of the dam for trait 1;
G_{D_2} = genotypic value of the dam for trait 2.

Figure 2. Path Coefficient Diagram Relating a Boar's Performance for a Reproductive Trait and His Littermate Brother's Performance for a Breeding Performance Trait

CHAPTER IV

RESULTS AND DISCUSSION

Variance Component Estimation

The analysis of variance for testicular and epididymidal traits, differing hormone concentrations and breeding performance traits can be found in Tables XIV through XVI. Sire nested within breed of sire is confounded with year-season farrowed. The group of Duroc sires used the first two breeding seasons were different from those used the subsequent three. A reduction in the degrees of freedom for the three way interaction of sire breed x dam breed x year-season farrowed was due to missing subclasses.

The sire breed x dam breed x year-season farrowed was not significant for any of the LH and testosterone levels or the boar breeding performance traits. Fent (1980) found for these data, that breed of boar by year-season farrowed was a significant source of variation for plasma testosterone levels three and four hours after GnRH injection. For the breeding performance traits, Buchanan and Johnson (1983) reported that the interaction of breeding season with breed of boar nested within breed of female was significant. The effect of sire nested within breed of sire was significant

TABLE XIV

LEAST SQUARES ANALYSES OF VARIANCE FOR TESTICULAR AND EPIDIDYMIDAL TRAITS

Trait[a]		TWT	CCW	CW	TTS	CCS	CS	TEPW	TEPS	SGT
Source[b]	d.f.	[c]M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.
Sea	3	4907.56	87.43	144.03*	352.02	220.71	317.96	353.38	1067.11	.004
BOS	3	6752.22+	113.91	2.75	622.24+	202.23	349.63	119.94	565.75	.007
BOD	3	3009.23	75.26	143.40*	216.57	119.75	137.08	397.65+	468.09	.003
BOS x BOD	9	10808.43*	101.62*	101.62*	587.31*	160.31	730.86	408.48*	1391.55	.007+
Sire (BOS)	33	2345.87	50.69	58.98	326.69	207.20	632.37	169.90	1211.05	.006+
Error	68	3093.46	53.46	49.18	285.23	202.25	617.20	172.38	1259.47	.003

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Total testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm number per gram of testis.

[b]Sea = Year-season farrowed; BOS = Breed of sire; BOD = Breed of dam; Sire (BOS) = Sire nested within breed of sire.

[c]Mean Square.

*P<.05.

+P<.10.

TABLE XV

LEAST SQUARES ANALYSES OF VARIANCE FOR LH AND TESTOSTERONE CONCENTRATIONS IN BOARS

Trait[b]		TE	TE1	TE2	TE3	TE4	LH	LH1	LH2	LH3	LH4
Source[a]	d.f.	M.S.[c]	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.
BOS	3	11.2	96.57^{+}	511.33*	164.26**	138.22**	0.32	51.32**	6.57$_{**}$	3.47^{+}	0.67
BOD	3	14.57	82.88^{+}	45.84	19.35	11.77	0.74	44.73*	26.22**	5.91$_{*}$	1.33
Sea	4	0.74	35.03	73.75	9.58	6.84	1.40^{+}	30.38*	15.46	4.10*	0.66
BOS x BOD	9	3.96	8.54	48.08	24.89	52.50^{+}	0.09	25.67*	7.12	1.11	0.22
BOS x Sea	11	2.96	16.25$_{*}$	144.08	56.73^{+}	9.47	0.69	13.55	6.03	1.41$_{*}$	0.39
BOD x Sea	12	5.13	69.77*	64.54	41.58	29.33	0.70	4.81	7.05	3.24*	0.94
BOS x BOD x Sea	22	6.36	29.70	36.27	40.19	43.55	0.46	9.96	4.19	1.19$_{*}$	0.37
Sire (BOS)	30	6.87	28.29	85.45	45.01	37.99	0.39	13.14	8.01^{+}	3.13*	0.98
Error	32	7.19	33.59	130.10	31.06	27.94	0.65	11.01	4.67	1.52	10.74

[a]BOS = Breed of Sire; BOD = Breed of dam; Sea = Year-season farowed; Sire (BOS) = Sire nested within breed of sire.

[b]TE = Basal plasma testosterone levels; TE1-TE4 = Plasma testosterone levels at hourly intervals after GnRH injection; LH = Basal plasma LH levels; LH1-LH4 = Plasma LH levels at hourly intervals after GnRH injection.

[c]Mean Square.

$^{**}P<.01$.

$^{*}P<.05$.

$^{+}P<.10$.

TABLE XVI

LEAST SQUARES ANALYSES OF VARIANCE FOR BOAR BREEDING PERFORMANCE TRAITS

Trait	Average Number of Services/Conception		Average Conception Rate
Source[a]	d.f.	M.S.[b]	M.S.
BOS	3	0.02	0.01
BOD	3	0.43	0.02
Sea	4	0.06	0 01
BOS X BOD	9	0.06	0.05
BOS X Sea	12	0.06	0.03
BOD X Sea	12	0.18**	0.07*
BOS X BOD X Sea	28	0.35	0.03
Sire (BOS)	31	0.06	0.04
Error		0.06	0.04

[a]BOS = Breed of sire; BOD = Breed of dam; Sea = Year-season farrowed; Sire (BOS) = Sire nested within breed of sire.

[b]Mean Square

**P<0.01

*P<0.05

+P<0.10

only for plasma LH levels at three hours after GnRH treatment, however this effect did approach significance ($P<0.10$) for LH levels at two hours after GnRH treatment and for sperm number per gram of testis.

A listing of the sire covariance and error covariance components can be found in Tables XXXII through XXXIV (Appendix). Sire variance component coefficients (k values) are located in Table XXXI (Appendix).

Heritability Estimation

Paternal half-sib heritability estimates for male reproductive traits were calculated. Testicular and epididymidal weights and sperm counts were taken on 120 boars representing 38 sires. Boar breeding performance was evaluated on 145 boars that were the progeny of 35 sires. Thirty-five sires were represented among the 128 boars for which endocrine response to GnRH treatment was measured. Boars were approximately seven months of age when evaluation began.

Heritability estimates and their standard errors are presented in Table XVII. The testicular and epididymidal traits had heritability estimates that are low to moderate in size, except for sperm number per gram of testis which had an estimate of 0.74 ± 0.523. This was the only heritability with a standard error smaller than the estimate. In another study, sperm concentration in boars of the five different breeds was found to have a full-sib

TABLE XVII

HERITABILITY ESTIMATES OF MALE REPRODUCTIVE TRAITS

Trait[a]	h^{2b}	SE[c]	Trait	h^2	SE
TWT	-0.40	.451	TE	-1.10	1.245
CCW	-0.08	.485	TE1	-0.42	1.268
CW	0.28	.510	TE2	-1.04	1.286
TTS	-0.21	.506	TE3	0.85	1.110
CCS	0.04	.494	TE4	0.71	1.135
CS	0.04	.494	LH	-1.26	1.282
TEPW	-0.02	.489	LH1	0.42	1.182
TEPS	-0.06	.486	LH2	1.20	1.037
SGT	0.74	.523	LH3	1.56	0.950
ANSC	0.06	.943	LH4	.66	1.144
ACR	.35	.935			

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Total testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm per gram of testis; ANSC = Average number of services per conception; ACR = Average conception rate; TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone level at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH-LH4 = Plasma LH levels at hourly intervals after GnRH injection.

[b]Paternal half-sib heritability estimate.

[c]Standard error of the estimate.

heritability estimate of 0.68 (Masek et al., 1979). Courot and Legault (1977) reported that testicular sperm reserves had a heritability estimate of 0.38±0.35.

In 65 Hereford bulls the heritability estimate of sperm per gram of testis was 0.32 (Johnson et al., 1974). A later report of that study indicated that sperm per gram of testis had a heritability estimate of -0.16±0.18 (Neely et al., 1982). The difference between these two estimates can be attributed to differences in sample size, with the latter having measurements on 578 bulls.

Testicular weight, caput-corpus epididymidal weight, total testicular sperm number, total epididymidal weight and total epididymidal sperm number all had negative estimates of the sire variance. Testis weight had a heritability estimate of 0.34±0.33 in boars of Large White breeding (Courot and Legault, 1977). Legault et al. (1977) reported a larger estimate for the purebred progeny of 16 Large White sires (h^2=0.73). Testicular weight and total testicular sperm had heritability estimates of 1.46 and 0.60, respectively in Hereford bulls. Neely et al. (1982) reported that total sperm in the testes had a heritability of 0.14±0.21, however after adjusting for differences in body weight at the time of measurement, the estimate was 0.06±0.20.

Total epididymidal weight had a heritability estimate of -0.02. This conflicts with the findings of Courot and Legault (1977) and Legault et al. (1979), who reported

heritability estimates of 0.38±0.35 and 0.35, respectively. The heritability estimate for total epididymidal sperm number was -0.06. Courot and Legault (1977) estimated a heritability that was positive (0.42±0.37), while Johnson et al. (1974) reported a heritability for epididymidal sperm number in bulls of 0.17.

Hormonal levels had heritabilty estimates that ranged from -1.26 to 1.56. All estimates in the parameter space had standard errors that were as large or larger than the estimate itself. Several traits had negative estimates of the sire variance (TE, TE1, TE2 and LH). This indicates a small additive variance for these traits. Wettemann et al. (1980) reported heritability estimates for plasma progesterone and plasma LH concentrations, in gilts, of 0.48±0.41 and 0.29±0.40, respectively.

In sheep that have been selected for LH response to a 5 microgram injection of LH-releasing hormone at 10 weeks of age, a heritability of 0.33 for LH response was reported (Land et al., 1981).

Heritability estimates for the breeding performance traits were low to moderate in size. This suggests that small to moderate progress could be made when selecting for average number of services per conception and average conception rate, however these estimates were not significantly different from zero.

Reproductive traits have been classified as being lowly

heritable. This may cause seed stock producers to relax selection pressure on reproductive traits because of the belief that little or no progress would be made. Reports from the Nebraska gene pool study have indicated that ovulation rate is moderately heritable (Cunningham et al., 1979). From this study, sperm per gram of testis may also be moderately heritable, indicating not all reproductive traits are lowly heritable. Reproductive productivity may be able to be increased at more rapid rates than generally thought.

Other than sperm number per gram of testis, the heritability estimates for testes and sperm measurements were generally low and most of the estimates had large standard errors. Larger studies may be necessary to better understand the genetics of these reproductive traits, however the cost of such a study and the time necessary for hormone evaluation are limiting factors.

Correlations of Testicular and Epididymidal Traits

Pooled within class, phenotypic and genetic correlations for testicular and epididymidal traits are presented in Table XVIII. In general, the phenotypic correlations were moderately large and positive. Correlations of testicular weight and testicular and epididymidal sperm number ranged from 0.536 to 0.595, while correlations of testicular weight with the epididymidal

TABLE XVIII

PHENOTYPIC AND GENETIC CORRELATIONS AMONG TESTICULAR AND EPIDIDYMIDAL TRAITS AND BASAL PLASMA HORMONE CONCENTRATIONS

	TWT	CCW	CW	TTS	CCS	CS	TEPW	TEPS	SGT	TE	LH
TWT[a]		.708[d]	.669	.541	.536	.542	.752	.595	.216[+]	.226[+]	.058[c]
CCW	-[e]		.680	.389	.696	.561	.920	.671	.151[+]	.041[c]	-.119[c]
CW	-	+		.464	.497	.673	.913	.670	.273	.094[c]	.002[c]
TTS	-	-	-.662 ±2.173		.582	.532	.465	.605	.910	.061[c]	.014[c]
CCS	-	-	-2.831 ±19.534	-4.547 ±31.203		.623	.653	.837	.433	-.013[c]	-.103[c]
CS	-	-	.757 ±2.744	1.624 ±7.713	-20.490 ±192.572		.672	.950	.368	.001[c]	-.016[c]
TEPW	-	-	+	-	+	-		.732	.230[+]	.073[c]	-.065[c]
TEPS	-	-	-	-	+	-	-		.431	-.004[c]	-.052[c]
SGT	-	-	-1.607 ±.3790	1.277 ±.6572	-1.463 ±9.912	-.042 ±22.175	-	-		.018[c]	.044[c]
TE	+	+	.224 ±1.465	-1.894 ±.3119	-3.070 ±18.623	-2.926 ±17.847	+		-	-.279	
LH	+	+	+	+	+	+	+	+	-		

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Caudal epididymidal weight; TTS = Testicular sperm number; CCS = Capus-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm per gram of testis; TE = Basal plasma testosterone level; LH = Basal plasma LH level.

[+]P<.10.

[c]P>.10, all phenotypic correlations not having a superscript are significant (P<.05).

[d]Genetic correlations below the diagonal, phenotypic correlations above the diagonal.

[e]Sign of the additive genetic covariance; correlation could not be estimated due to one of the corresponding sire variance estimates being negative.

weights ranged from 0.669 to 0.752. This indicates that boars with heavier testes also tended to have heavier epididymial weights and more epididymidal and testicular sperm. These correlations are larger than those reported by Fent (1980), but correlations of breed averages for testicular and epididymidal traits were similar in magnitude. Wilson et al. (1977) found phenotypic correlations of moderate size for testicular and epididymidal traits except for those associated with caput-corpus epididymidal weight which were small and non-significant. Almquist and Amann (1961) reported that testis weight was positively correlated with epididymidal weight and total testicular sperm (0.82 and 0.62, respectively) in bulls of dairy breeding. These were similar to the correlations of testicular weight and total testicular sperm number reported in Hereford bulls (r=0.73, Johnson et al., 1974; r=0.74, Neely et al., 1982). Both studies reported a correlation of similar magnitude (0.91 and 0.83, respectively) as that reported here for total testicular sperm number and sperm per gram of testis (0.91). The phenotypic correlations of testicular and epididymidal traits with basal levels of LH and testosterone were small and non-significant. This may indicate that testicular and epididymidal traits are not influenced by different circulating plasma levels of LH or testosterone after males have reached puberty. Lunstra et al. (1978) studied 31 bulls (7-13 months of age) of five different breed groups

and found that scrotal circumference was significantly correlated to plasma LH (0.44) and testosterone (0.51).

The estimates of genetic correlation for testicular, epididymidal and basal hormone levels ranged from -20.49 to 1.624. Genetic correlations that were within the parameter space had the same sign as their corresponding phenotypic correlations except for the correlations of sperm per gram of testis with cauda sperm number and basal plasma testosterone and total testicular sperm with cauda epididymidal weight. Traits that have phenotypic and genetic correlations that are different in sign may be affected by genetic and environmental influences through different physiological mechanisms (Falconer, 1981). However, the genetic correlations in this study were not significantly different from zero. Over half of the genetic correlations could not be estimated due to negative estimates for the sire variance for one or both of the corresponding traits.

Correlations Among Plasma LH and Testosterone Levels

Pooled within class phenotypic and paternal half-sib genetic correlations are presented in Table XIX. Except for basal plasma LH and the LH level recorded one hour after GnRH administration, each plasma level of a particular hormone was positively related to the subsequent sample

TABLE XIX

PHENOTYPIC AND GENETIC CORRELATIONS FOR TESTOSTERONE AND CONCENTRATIONS IN BOARS

	TE	TE1	TE2	TE3	TE4	LH	LH1	LH2	LH3	LH4
TE[a]		.501**	.229[d]	.409*	.265	.265*	-.212	-.268	-.178	.121
TE1	-[e]		.362*	.591**	.274*	.361*	-.027	-.145	-.081	-.047
TE2	-	+		.628**	.425*	-.005	.290	.164	.230	.176**
TE3	+	+	-		.515*	.121	.260*	.189**	.266*	.253**
TE4	+	+	-	.209 ±.709		.288	.375*	.476**	.418*	.513**
LH	-	-	-	-	-		-.180	.230**	.215**	.526**
LH1	+	-	-	-.723 ±1.404	.429 ±5.346	+		.697**	.537**	.209
LH2	+	-	-	-.226 ±.616	-.009 ±.675	+	.103 ±.853		.895**	.689**
LH3	+	-	-	-.164 ±.544	.257 ±.503	+	.780 ±.558	.941 ±.066		.752**
LH4	-	-	-	.326 ±.897	.002 ±.106	+	1.67 ±1.592	.837 ±.748	1.139 ±.299	

[a]TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone levels at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH1-LH4 = Plasma LH level at hourly intervals after GnRH injection.

**P<.01.

*p<.05.

[d]Genetic correlations below the diagonal, phenotypic correlations above the diagonal.

[e]Sign of the additive genetic covariance correlation could not be estimated due to one or both of the corresponding sire variance estimates being negative.

concentrations. Testosterone levels four hours after GnRH injection were positively related to each LH measurement after GnRH treatment. Testosterone levels at one hour after GnRH treatment show moderate positive association with the basal level of LH. All other correlations among plasma testosterone and LH levels were not significant. Other studies have shown that basal plasma LH concentrations in boars were positively related to testosterone one hour after GnRH injection (r=0.22, Welsh and Johnson, 1978; r=0.26, Welsh and Johnson, 1979). In gilts, 30 days post breeding, basal plasma LH concentrations were found to have a small association (r=-0.03) with basal plasma progesterone (Wettemann et al., 1980).

In Angus bulls, LH concentration showed greater association with testosterone at 1 (r=0.64) and 1.5 hours (r=0.60) after GnRH treatment than at 0.5 (r=0.39) and 2 hours (r=0.35) after treatment (Minton, 1980). This is somewhat different than the findings of Welsh and Johnson (1978), who found the relationship of basal plasma LH concentrations to be smaller with testosterone levels at one hour after GnRH treatment (r=0.34). Bulls of different beef breeds were found to have a moderate positive association between basal plasma LH and testosterone (r=0.38, Lunstra et al., 1978). This conflicts with the findings of Welsh and Johnson (1978) and Minton (1980), who reported non-significant correlations between basal LH and testosterone concentrations. Paternal half-sib genetic correlations

among differing hormonal concentrations were calculated (Table XIX). Of the correlations that were estimable, only two were outside the parameter space (LH4 with LH1 and LH3). The genetic correlations of LH1 and LH3, LH2 and LH3, and LH3 and LH4 are significantly different from zero. Each of these correlations was large and positive (0.780, 0.941 and r=0.837, respectively). Genetic correlations of this sign and magnitude may indicate that a large portion of the segregating genes that influence one trait control the other trait in a similar manner. The genetic correlations of LH3 with TE3 (-0.164 ± 0.106) and LH4 with TE4 (0.002 ± 0.106) were small and were not significantly different from zero. This may suggest that the genetic control of LH levels at three and four hours after GnRH injection may have little pleiotropic effect on testosterone levels at the respective time periods. All other correlations were not significantly different from zero. Wettemann et al. (1980) found that the genetic correlation between basal plasma LH and progesterone in gilts 30 days postbreeding was small and did not differ from zero (0.14 ± 0.86).

Genetic and Phenotypic Relationships for Breeding Performance Traits in Boars

Pooled, within class, phenotypic and paternal half-sib genetic correlations for breeding performance traits are

located in Table XX.

TABLE XX

PHENOTYPIC AND GENETIC CORRELATIONS FOR BREEDING PERFORMANCE TRAITS IN BOARS

	Average No. of Services/Conception	Average Conception Rate
Average No. of Services/Conception		-.724*
Average Conception Rate	-2.502±54.610[a]	

*P<.01

[a]Phenotypic correlation above the diagonal, genetic correlation below the diagonal.

The phenotypic correlation between average conception rate and average number of services per conception was -0.724. This indicates that as a boar needs fewer services to settle females during an eight week breeding season, his conception rate for the breeding season tended to be larger. The corresponding genetic correlation was negative (2.502±54.61) and outside the parameter space.

Relationships of Testicular Traits, Hormone Concentrations and Breeding Performance of Boars with Age and Weight at Puberty of Littermate Gilts

Pooled, within class, phenotypic correlations between testicular traits in boars and age and weight at puberty in littermate gilts are presented in Table XXI. Cauda epididymidal weight and total epididymidal weight were positively correlated with weight at puberty (0.210 and 0.194, respectively). This implies that boars with heavier epididymides tend to have sisters that are somewhat heavier when reaching puberty, and consequently may be older at puberty. Total testicular sperm number and sperm per gram of testis were found to have significant correlations of -0.205 and -0.207, respectively, with weight at puberty suggesting that boars with more gonadal sperm tended to have sisters that weighed less when reaching puberty and were younger as well. It has been reported that, in swine, testicular and epididymidal weight were negatively correlated with age at puberty (-0.02 and -0.14, respectively) and positively correlated with ovulation rate (0.19 and 0.15, respectively) (Schinckel, 1980). In mice selected for ovulation rate, the partial correlation between ovulation rate and testis weight was 0.82 (Land, 1973). In an extensive examination of eight breeds of beef cattle, it

TABLE XXI

POOLED WITHIN CLASS PHENOTYPIC CORRELATIONS OF TESTICULAR TRAITS WITH AGE AND WEIGHT OF PUBERTY IN LITTERMATE GILTS

Testicular Traits[a]	Age at Puberty	Weight at Puberty
TWT	-.028	.001
CCW	-.029	.138
CW	.065	.210*
TTS	-.276	-.205*
CCS	-.014	-.136
CS	-.068	-.111
TEPW	.017	.194*
TEPS	-.054	-.136
SGT	-.019	-.207*

*P<.05.

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Total testicular sperm; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm number per gram of testis.

was found that breeds that have bulls with greater scrotal circumference will have heifers that reach puberty at a younger age (Lunstra, 1982).

Genetic correlations (Table XXII) were computed as discussed in Chapter III. The use of this formula ($r_g=2r_{FS}/h_1h_2nb$) assumes that the sign of the phenotypic and genetic covariance are the same. Genetic correlations not calculated were those that had negative heritability estimates for the corresponding male traits. Since testes weight had a negative estimate for the sire variance, the heritability estimate used was the weighted average heritability estimate reported in Chapter II. The heritability estimates for age (0.19 ± 0.09) and weight at puberty (0.35 ± 0.12) were those published by Hutchens (1980) for these data. It should be mentioned that except for sperm number per gram of testis, these heritability estimates did not differ significantly from zero. Because of this, care should be taken when interpreting these genetic correlation estimates. Cauda epididymidal weight was found to have a genetic correlation of 0.763 with weight at puberty, while the genetic correlation of sperm per gram of testis with weight at puberty was -0.462. It would appear that selection for gilts that are heavier at puberty may cause increases in cauda epididymidal weight and decrease testes sperm concentration in boars. Schinckel (1980) found that if the heritability for testes weight is between 0.3 and 0.6, then the genetic correlation of testes

TABLE XXII

GENETIC CORRELATIONS BETWEEN TESTICULAR TRAITS AND AGE AND WEIGHT AT PUBERTY IN LITTERMATE GILTS

Testicular Traits[a]	Age at Puberty	Weight at Puberty
TWT[b]	-.087	.002
CCW	c	c
CW	.298	.763
TTS	c	c
CCS	-.170	-1.307
CS	-.825	-1.067
TEPW	c	c
TEPS	c	c
SGT	-.054	-.462

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm number per gram of testis.

[b]Literature heritability estimate was used to calculate the genetic correlation.

[c]Correlation could not be estimated due to the male trait having a negative estimate of the additive genetic variance component.

weight and ovulation rate would be included in the interval of 0.39 to 0.65.

In mice selected for testes weight, the genetic correlation with ovulation rate of primiparous females was 0.50±0.18, while the genetic correlation with ovulation rate of nulliparous females was 0.25±0.20 (Islam and Hill, 1976). Joakimsen and Baker (1977) found that for mice selected for large and small litter size, testicular weight showed a positive relationship to an increase in litter size. In beef cattle it has been demonstrated that scrotal circumference has a negative genetic relationship (-.71) with age puberty in heifers (Brinks et al., 1978).

Phenotypic correlations of plasma LH and testosterone concentrations with age and weight at puberty can be found in Table XXIII. Age and weight at puberty were positively correlated with testosterone levels at one (0.197), two (0.208) and three hours (0.232) after GnRH treatment, while weight at puberty was also positively associated with basal levels of testosterone (0.259). It would appear that boars that had high levels of testosterone at the indicated sampling periods tended to have sisters that were older and heavier when reaching puberty. The correlation of age at puberty with LH concentrations at one hour after treatment, and the correlation of weight at puberty with basal plasma levels of LH approached significance (-0.179 and 0.198, respectively; $P<0.10$). This may imply that boars with higher basal LH levels had sisters that were heavier at

TABLE XXIII

POOLED WITHIN CLASS PHENOTYPIC CORRELATIONS BETWEEN BOAR HORMONE CONCENTRATIONS AND AGE AND WEIGHT AT PUBERTY IN LITTERMATE GILTS

Hormone Levels	Age at Puberty	Weight at Puberty
TE[d]	.160	.259*
TE1	.197*	.217*
TE2	.208*	.206*
TE3	.232*	.371**
TE4	-.029	.190+
LH	.014	.198+
LH1	-.179+	-.005
LH2	-.044	.155
LH3	-.072	.126
LH4	-.070	.117

**P<.01.

*P<.05.

+P<.10.

[d]TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone level at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH1-LH4 = Plasma LH level at hourly intervals after GnRH injection.

puberty, however boars that had higher LH concentrations at one hour after GnRH injection tended to have sisters that were younger at puberty. It has been reported that breeds of sheep that are noted for their prolificacy have higher levels of gonodotrophic hormones in the blood at a young age and the males of these breeds have a more rapid testes growth rate (Land, 1981).

Genetic correlations among age and weight at puberty and boar hormone concentrations are reported in Table XXIV. The correlations of age and weight at puberty with testosterone concentrations at three hours after GnRH injection were large and positive (0.603 and 0.766, respectively) while LH levels at one hour after treatment were negatively correlated with age and weight at puberty (-0.661 and -0.147, respectively). These data suggest that if one of the goals of selection program was to decrease the age when females first enter the breeding herd, monitoring LH levels in the males may be more advantageous than monitoring testosterone levels.

Phenotypic and genetic correlations of boar breeding performance traits with age and weight at puberty in gilts are located in Tables XXV and XXVI. The phenotypic correlations were small and not significant, suggesting that the age and weight of a gilt when she reaches puberty have little correlation with her brother's ability to get sows pregnant. Genetic correlations were calculated (Table XXVI), but since the phenotypic correlations were not

TABLE XXIV

GENETIC CORRELATIONS AMONG BOAR HORMONE CONCENTRATIONS AND AGE AND WEIGHT AT PUBERTY IN LITTERMATE GILTS

Hormone Levels	Age at Puberty	Weight at Puberty
TE[a]	b	b
TE1	b	b
TE2	b	b
TE3	.603	.766
TE4	-.082	.423
LH	b	b
LH1	-.661	-.147
LH2	-.096	.269
LH3	-.138	.192
LH4	-.206	.274

[a]TE = Basal testosterone level; TE1-TE4 = Plasma testosterone levels at hourly intervals after GnRH injection; LH = Basal LH level; TE1-TE4 = Plasma LH level at hourly intervals after GnRH injection.

[b]Correlation could not be estimated due to the negative estimate additive genetic variance component for the male trait.

TABLE XXV

POOLED WITHIN CLASS PHENOTYPIC CORRELATIONS BETWEEN BOAR BREEDING PERFORMANCE TRAITS AND AGE AND WEIGHT AT PUBERTY IN LITTERMATE GILTS

	Age at Puberty	Weight at Puberty
Average Number of Services/Conception	-.124[a]	-.084
Average Conception	-.101	.098

[a]All phenotypic correlations are not significant (P>.15).

TABLE XXVI

GENETIC CORRELATIONS BETWEEN BOAR BREEDING PERFORMANCE TRAITS AND AGE AND WEIGHT AT PUBERTY IN LITTERMATE GILTS

	Age at Puberty	Weight at Puberty
Average Number of Services/Conception	-1.211	-.653
Average Conception	-.409	.315

significantly different from zero they are difficult to interpret.

Relationships of Testicular Traits and Hormone Concentrations with Breeding Performance Traits in Littermate Boars

Phenotypic correlations among testicular traits and breeding performance traits can be found in Table XXVII. Correlations of testicular weight, cauda epididymidal sperm number and total epididymidal sperm number were positively correlated with average conception rate (0.384, 0.453 and 0.443, respectively). This suggests that boars with heavier testes and more epididymidal sperm tended to have brothers that settled more females during the eight week breeding season.

Genetic correlations for testicular traits with breeding performance traits are in Table XXVIII. The genetic correlations among traits of littermate brothers were calculated using an approximation formula as presented in Chapter III. The formula ($r_g=2r_B/h_1h_2$) assumes that the phenotypic and genetic covariance have the same sign as well as the environmental correlation being zero. Genetic correlations not calculated were those in which the corresponding testicular trait or hormone concentration had a negative heritability estimate. Only the genetic correlations of cauda epididymidal weight, total

TABLE XXVII

POOLED WITHIN CLASS PHENOTYPIC CORRELATIONS BETWEEN TESTICULAR TRAITS AND LITTERMATE'S BREEDING PERFORMANCE

Testicular Traits	Average No. Services/ Conception	Average Conception Rate
TWT[b]	-.164	.384*
CCW	.038	.013
CW	-.041	.138
TTS	.007	.258
CCS	-.163	.291
CS	-.265	.453*
TEPW	-.002	.084
TEPS	-.256	.443*
SGT	.004	.268

*P<.05.

[b]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Total testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm per gram of testis.

TABLE XXVIII

GENETIC CORRELATIONS AMONG TESTICULAR TRAITS AND LITTERMATE'S BREEDING PERFORMANCE

Testicular Traits[a]	Average No. Services/ Conception	Average Conception Rate
TWT[a]	-1.715	1.662
CCW	b	b
CW	-.633	.882
TTS	b	b
CCS	-6.65	4.919
CS	-10.819	7.657
TEPW	b	b
TEPS	b	b
SGT	.040	1.053

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Total testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm per gram of testis.

[b]Correlation could not be estimated due to the negative estimate of the additive genetic variance component for the associated testicular trait.

epididymidal weight and sperm number per gram of testis with the average number of services per conception, along with the correlation of cauda epididymidal weight with average conception rate are within the parameter space. The correlations were fairly strong for cauda epididymidal weight and breeding performance, but should be viewed with caution since many of the correlation estimates were not reasonable.

Pooled within class phenotypic correlations of LH and testosterone concentrations before and after GnRH treatment with the full-sib's breeding performance are presented in Table XXIX. LH levels at three and four hours after GnRH injection were positively correlated with average conception rate (0.341 and 0.354, respectively), and approached significance ($P<0.10$). This implies that boars with high LH levels at three and four hours after GnRH injection may have had brothers that settled more females during the eight week breeding season.

Genetic correlations among LH and testosterone plasma concentrations before and after GnRH treatment with their full-sib's breeding performance are in Table XXX. Again, few of the correlations were in the parameter space. Those that had absolute values less than 1.0 were large and indicated that selection for increased LH or testosterone levels may have a favorable impact on conception rate.

TABLE XXIX

POOLED WITHIN CLASS PHENOTYPIC CORRELATIONS BETWEEN BOAR HORMONE CONCENTRATIONS AND LITTERMATE'S BREEDING PERFORMANCE

Hormone Levels[a]	Average No. Services/ Conception	Average Conception Rate
TE	.082	-.018
TE1	-.110	.115
TE2	-.135	.131
TE3	-.147	.062
TE4	-.194	.177
LH	.209	-.044
LH1	-.350	.173
LH2	-.158	.240
LH3	-.288	.341+
LH4	-.265	.354+

+P<.10.

[a]TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone levels at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH1-LH4 = Plasma LH level at hourly intervals after GnRH injection.

TABLE XXX

GENETIC CORRELATIONS AMONG BOAR HORMONE CONCENTRATIONS AND LITTERMATE'S BREEDING PERFORMANCE

Hormone Levels	Average No. Services/ Conception	Average Conception Rate
TE[a]	b	b
TE1	b	b
TE2	b	b
TE3	-1.302	.227
TE4	-1.880	.710
LH	b	b
LH1	-4.100	.902
LH2	-1.178	.741
LH3	-1.883	.923
LH4	-2.663	1.473

[a]TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone level at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH1=LH4 = Plasma LH levels at hourly intervals after GnRH injection.

[b]Correlation could not be estimated due to the negative additive genetic variance component for associated hormone concentration.

Discussion

After studying the results, it can be seen that selecting gilts that reach puberty at a younger age may cause a slight increase in weight at puberty (r_g=-0.03) (Hutchens, 1980). In their male relatives, increases in LH levels are possible. Basal plasma LH levels were positively related to testes weight (genetic covariance = 0.216) and testicular sperm number (genetic covariance = 0.307). Basal plasma LH levels are negatively associated with basal plasma levels of testosterone (genetic covariance = -0.232). Basal testosterone levels were negatively associated with testicular sperm number and sperm per gram of testis (genetic correlations are -1.89 and -0.279, respectively), but positively associated with testes weight (genetic covariance = 0.216). Basal testosterone levels were positively associated with testosterone levels four hours after treatment (genetic covariance = 2.116), however testosterone levels at four hours after treatment were negatively associated with the age at puberty of female relatives (r_g = -0.082). This suggests that selecting gilts that reach puberty at a younger age may cause testicular weight and testicular sperm number to increase in their male relatives. A problem may exist with the correlated response of testosterone and associated traits, however the relationships encountered are somewhat speculative.

LH levels at four hours after treatment (LH4) were

shown to have a moderately large heritability estimate (.66). LH4 was also positively correlated with average conception rate (r_g=1.473) and basal plasma LH concentration (LH) (genetic covariance = 0.264). LH was positively associated with all the testicular traits except total epididymidal sperm number and sperm number per gram of testis (Table XVIII). This may imply that selecting males for increased LH levels at four hours after GnRH injection may cause increases in gonadal weight and sperm counts in related boars. Also, related males may possibly settle more females during the breeding season. Another possibility is a decrease in age at puberty in female relatives, as discussed earlier.

In the commercial swine industry, reproductive efficiency is the one trait with the most impact on profit or loss. However, most research efforts and the subsequent recommendations made to the commercial producer have dealt mainly with growth and growth related traits. There has been no conclusive documentation on what can be expected when selecting for reproductive efficiency. However, as capital investment increases, increases in production may have to come from the existing breeding herd and not from expansion. Boars will be expected to settle a higher percent of the female herd, while those gestating females will be expected to farrow larger litters that are healthy and vigorous. Unfortunately, the guidelines for such programs are not yet formed.

Litter size has been characterized as a lowly heritable trait (Warwick and Legates, 1979). However, it has been shown in mice that increases in litter size are possible (Joakimsen and Baker, 1977). They found that testes weight showed positive response to selection for increased litter size. Land (1973) and Islam et al. (1976) showed that ovulation rate and testes weight were favorably related in mice. Schinckel (1980) reported similar findings in swine. Brinks et al. (1978) reported a genetic correlation of -0.71 for scrotal circumference of beef bulls with age at puberty in half-sib heifers. In this study, testes weight of boars and age at puberty of full-sib gilts showed a similar relationship, though smaller in magnitude (r_g=-0.087). Also, testes weight showed favorable relationships with average conception rate (r_g=1.66) and basal testosterone and LH levels (positive genetic covariance). Differing LH and testosterone plasma levels showed optimum relationships with age at puberty (TE4, LH1, LH2, LH3 and LH4 with age at puberty) and breeding performance (TE and LH with average number of services per conception and TE1-TE4 and LH1-LH4 with average conception rate). TE3, TE4 and LH4 were reported earlier to have large heritablities (0.85, 0.71 and 0.66, respectively). Land (1981) reported that LH concentration in sheep was moderately heritable (0.33). Also, breeds of sheep noted for prolificacy had higher circulating LH levels and males with more rapid testes

growth than those breeds that are not as prolific. If we can extrapolate across species we can suggest that selecting for increased litter size, decreased age at puberty in gilts, or testes size or weight will not only cause a desired response in the sex of selection but may also bring about favorable changes in the opposite sex. Selection for increased litter size could bring about increases in testes size and weight in related males. This could cause an increase in the average conception rate. If selection for a decrease in age at puberty of gilts is practiced, increases in testes weight, total testicular sperm number and average conception rate of related males could be expected.

Selecting for some of these traits (e.g., litter size) will not bring about as rapid a change as desired, however over time favorable changes will become evident and profit should increase. Favorable changes in reproductive efficiency must be made to be able to meet the high costs of production. This change could be a slow one, but the change should bring about a relatively constant increase in the desired trait(s) and subsequently bear fruit by increasing production efficiency.

CHAPTER V

SUMMARY

Data for these analyses were accumulated during the study of a four-breed diallel mating system. Purebred and two-breed cross litters were produced for five consecutive seasons (Fall 1976 - Spring 1978). Reproductive traits were measured on littermate boars for all five seasons, while age and weight at puberty were recorded for littermate gilts the first four seasons. Calculation of heritability estimates for male reproductive traits, correlation estimates among these traits, plus correlation estimates among male and female reproductive traits were the main objective of this study.

Two boars from each litter farrowed were left intact. Selection was based on individual 42 day weight, with the two heaviest boars not being castrated. After completing gain test, littermate boars were randomly allocated to either the Nutrition-Physiology Research Center for endocrine analysis, or to the Southwestern Livestock and Forage Research Station for breeding performance evaluation. Gilts were raised in total confinement adjacent to boar pens or in pasture lots with littermate barrows. Gilts were removed from gain test at 90.7 kgs and monitored for first

estrus as detected by a teaser boar. Age and weight of the gilts were recorded when first estrus was detected.

Records of 120, 128 and 145 boars were available for genetic parameter estimation for testicular characteristics, differing hormone levels before and after GnRH injection and breeding performance traits, respectively. Paternal half-sib heritability estimates for these traits were calculated. Five testicular traits (testes weight, caput-corpus epididymidal weight, total testicular sperm, total epididymidal weight and total epididymidal sperm number) had negative estimates of the sire variance. Caput-corpus epididymidal sperm number and cauda epididymidal sperm number had small heritability estimates (0.04 and 0.04, respectively). The heritability estimate for cauda epididymidal weight was moderate in size (0.28), while the estimate for sperm per gram of testis was large (0.74). Average number of services per conception and average conception rate had heritability estimates of 0.06 and 0.35, respectively. The heritability estimates of testosterone concentrations at three and four hours and LH levels four hours after GnRH injection fell within the parameter space (0.85, 0.71 and 0.66, respectively).

Genetic correlations among testicular traits and basal plasma LH and testosterone concentrations ranged from -20.49 to 1.624. Genetic correlations of differing hormone concentrations ranged from -0.723 to 1.670. Correlations among plasma LH levels at two hours after GnRH injection

with LH levels at three (0.941) and four hours (0.837) after GnRH treatment were significantly different from zero. So were LH levels at one hour after injection with LH concentrations at three hours after GnRH treatment (0.780).

Pooled, within class phenotypic and genetic correlations among testicular traits, differing plasma hormone concentrations and breeding performance traits of boars with age and weight at puberty of gilts were estimated. Also, pooled, within class phenotypic and genetic correlations of testicular traits and plasma hormone levels with breeding performance traits of full-sib boars were estimated. Cauda epididymidal weight and total epididymidal weight were positively correlated with weight at puberty (0.210 and 0.194, respectively), while total testicular sperm number and sperm number per gram of testis were negatively correlated with weight at puberty (-0.205 and -0.207, respectively). The corresponding genetic correlations of cauda epididymidal weight and sperm number per gram of testis with weight at puberty (0.763 and -0.462) were in the range of the parameter space.

Phenotypic correlations of age at puberty with testosterone levels at one, two and three hours after GnRH injection (0.197, 0.208 and 0.232, respectively) were significant. Correlations of weight at puberty with testosterone concentrations at zero, one, two and three hours after GnRH treatment were also significant (0.259,

0.217, 0.206 and 0.371, respectively). Pooled within class phenotypic correlations among boar breeding performance and age and weight at puberty ranged from -0.124 to 0.098 and were not significant. Pooled, within class phenotypic correlations were calculated for testicular traits and differing LH and testosterone concentrations after GnRH injection with the full-sib's breeding performance records.

Cauda epididymidal sperm number and total epididymidal sperm number were positively correlated with average conception rate (0.453 and 0.443, respectively), however the corresponding genetic correlations were not contained within the parameter space (7.657 and 6.114, respectively). Phenotypic correlations among average conception rate with LH concentrations at three and four hours after treatment (0.341 and 0.354, respectively) approached significance ($P<0.10$). Of the two corresponding genetic correlations, only the correlation of average conception rate with LH concentrations three hours after GnRH treatment (0.923) was in the parameter space.

Reports from the Nebraska gene pool population and this study have found that gonadal traits (e.g., ovulation rate and sperm per gram of testis) are at least moderately heritable. This demonstrates that not all reproductive traits are lowly heritable. However, how selection for these moderately heritable traits may change reproductive efficiency is not yet clear. The amount of additive genetic variation of plasma LH and testosterone concentrations is

not yet fully understood, but does not look promising (negative sire variance component estimates for basal plasma LH and testosterone concentrations). Relationships among male and female sex-limited traits are favorable for some traits, however the small phenotypic correlations and the "puzzling" genetic correlations in this study, and other reports as well, suggest that these relationships may not be as enticing as once hoped. Until further understanding of how reproductive physiological mechanisms of different sexes may be related, direct selection for reproductive proficiency in each sex should be the method of practice until such time as the appropriate correlated selection methods are more comprehensive.

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APPENDIX

TABLE XXXI

VARIANCE COMPONENT COEFFICIENTS AND DEGREES OF FREEDOM FOR TESTES HORMONE AND BREEDING PERFORMANCE TRAITS

	d.f.	k
Testis Traits		
Sire (BOS)	33	1.652
Error	68	
Hormone Traits		
Sire (BOS)	30	1.667
Error	32	
Breeding Performance Traits		
Sire (BOS)	31	1.957
Error	41	

TABLE XXXII

SIRE VARIANCE COMPONENTS AND SIRE AND RESIDUAL COVARIANCE COMPONENTS FOR TESTICULAR TRAITS

	TWT	CCW	CW	TTS	CCES	CES	TEPW	TEPS	SGT	TE	LH
TWT[a]	-281.900[b]	208.745[c]	261.073	508.289	424.243	450.937	549.142	703.089	.705	31.409	-2.701
CCW	-29.911[d]	-1.046	34.869	48.073	72.392	101.845	88.331	174.236	.065	1.927	1.592
CW	-30.034	16.965	3.695	54.956	-7.439	117.260	84.048	166.813	.112	1.663	.011
TTS	-176.935	-12.011	-5.034	15.632	139.608	223.080	103.029	362.688	.142	2.594	.201
CCS	-64.891	-19.416	-7.439	-24.580	1.870	220.012	220.012	422.258	-.361	-.468	-1.232
CS	-112.460	-31.985	3.139	-14.630	-63.834	5.720	219.105	837.208	.537	.087	.328
TEPW	-59.945	-2.839	1.902	-17.045	63.834	-28.672	-.937	341.049	.177	2.425	-.723
TEPS	-177.351	-51.401	-4.126	-39.211	11.409	-7.203	-55.527	-.015	.899	-.382	-1.561
SGT	-.124	-.053	-.009	.142	-.056	-.001	-.037	-.059	.001	.003	.002
TE	.216	.439	-.250	-4.364	-2.446	-3.871	1.511	-6.316	-.014		
LH	4.531	.877	.320	.307	.337	.898	1.197	-.560	-.001		

[a]TWT = Testicular weight; CCW = Caput-corpus epididymidal weight; CW = Cauda epididymidal weight; TTS = Testicular sperm number; CCS = Caput-corpus epididymidal sperm number; CS = Cauda epididymidal sperm number; TEPW = Total epididymidal weight; TEPS = Total epididymidal sperm number; SGT = Sperm per gram of testis; TE = Basal plasma testosterone level; LH = Basal plasma LH level.

[b]Sire variance component on the diagonal.

[c]Residual covariance component above the diagonal.

[d]Sire covariance component below the diagonal.

TABLE XXXIII

SIRE VARIANCE COMPONENTS AND SIRE AND RESIDUAL COVARIANCE COMPONENTS OF BOAR HORMONE CONCENTRATIONS

	TE	TE1	TE2	TE3	TE4	LH	LH1	LH2	LH3	LH4
TE[a]	-.193[b]	7.788[c]	7.008	6.113	3.752	.571	-1.886	-1.552	-.588	.278
TE1	-1.013[d]	-3.179	23.958	19.091	8.403	1.678	-.513	-1.813	-.577	-.235
TE2	-.656	10.119	-26.784	39.950	25.593	-.049	10.955	4.033	3.225	1.725
TE3	2.116	.521	1.256	8.368	.209	.539	4.802	2.271	1.827	1.212
TE4	2.526	1.728	-8.026	1.479	6.035	1.224	6.569	5.438	2.719	2.325
LH	-.232	-1.334	-.262	-.375	-.266	-.155	.478	.400	.213	.363
LH1	.863	-1.283	-8.414	-2.368	-1.194	.683	1.282	4.998	2.196	.596
LH2	.882	-.408	-5.771	.924	-.033	.234	.166	2.004	2.383	1.277
LH3	.593	-.230	-3.062	-.468	.620	.264	.868	1.310	.967	.795
LH4	-.149	-.444	-1.692	-.360	-.021	.004	.720	.452	.428	.146

[a]TE = Basal plasma testosterone level; TE1-TE4 = Plasma testosterone level at hourly intervals after GnRH injection; LH = Basal plasma LH level; LH1-LH4 = Plasma LH level at hourly intervals after GnRH injection.

[b]Sire variance component on the diagonal.

[c]Residual covariance component above the diagonal.

[d]Sire covariance component below the diagonal.

TABLE XXXIV

SIRE VARIANCE COMPONENTS AND SIRE AND RESIDUAL COVARIANCE COMPONENTS FOR BOAR BREEDING PERFORMANCE TRAITS

	Average No. Services/ Conception	Average Conception Rate
Average No. Services/ Conception	.056[a]	-.038[b]
Average Conception Rate	-.032[c]	.039

[a]Sire variance components on the diagonal.

[b]Residual covariance components above the diagonal.

[c]Sire covariance components below the diagonal.

TABLE XXXV

DISTRIBUTION OF GILTS USED FOR CORRELATION ANALYSIS WITH BOAR TESTES AND HORMONE TRAITS

Breed	Spring 1977	Fall 1977	Spring 1978	Fall 1978
Duroc (D)	5	6	4	8
Yorkshire (Y)	3	1	0	4
Landrace (L)	5	6	2	3
Spot (S)	5	5	9	9
DY	4	9	9	9
DL	2	7	12	8
DS	14	7	2	9
YL	5	8	6	10
YS	10	7	0	10
LS	12	4	6	9
	65	60	50	79

TABLE XXXVI

DISTRIBUTION OF GILTS USED FOR CORRELATION ANALYSIS WITH BOAR BREEDING PERFORMANCE

Breed	Spring 1977	Fall 1977	Spring 1978	Fall 1978
Duroc (D)	8	8	9	5
Yorkshire (Y)	9	6	5	5
Landrace (L)	10	9	5	5
Spot (S)	9	11	2	2
DY	9	10	6	6
DL	6	10	9	9
DS	9	7	6	6
YL	4	8	7	7
YS	9	6	9	9
LS	7	8	11	11
	80	83	69	65

TABLE XXXVII

DISTRIBUTION OF LITTERS USED FOR CORRELATION ANALYSIS OF BOAR TESTIS AND HORMONE TRAITS AND AGE AND WEIGHT AT PUBERTY IN GILTS

Breed	Spring 1977	Fall 1977	Spring 1978	Fall 1978
Duroc (D)	2	3	1	3
Yorkshire (Y)	1	1	0	1
Landrace (L)	2	2	1	1
Spot (S)	2	2	3	3
DY	2	3	3	3
DL	1	2	4	2
DS	4	3	1	3
YL	3	2	2	4
YS	3	3	0	3
LS	3	2	2	4
	23	23	17	17

TABLE XXXVIII

DISTRIBUTION OF LITTERS USED FOR CORRELATION ANALYSIS OF AGE AND WEIGHT AT PUBERTY OF GILTS AND BOAR BREEDING PERFORMANCE

Breed	Spring 1977	Fall 1977	Spring 1978	Fall 1978
Duroc (D)	3	3	3	2
Yorkshire (Y)	2	3	2	1
Landrace (L)	3	3	3	3
Spot (S)	3	3	2	3
DY	4	3	2	4
DL	2	3	3	3
DS	3	3	3	2
YL	2	2	3	1
YS	3	3	3	3
LS	3	3	3	2
	28	29	27	24

TABLE XXXIX

DISTRIBUTION OF LITTERS USED FOR CORRELATION ANALYSIS OF BOAR HORMONE AND TESTES TRAITS AND BOAR BREEDING PERFORMANCE

Breed	Spring 1977	Fall 1977	Spring 1978	Fall 1978	Spring 1979
Duroc (D)	2	2	1	3	2
Yorkshire(Y)	2	2	0	3	0
Landrace (L)	1	1	1	1	0
Spot (S)	2	1	0	2	2
DY	1	3	2	2	2
DL	2	3	3	3	3
DS	3	3	1	2	1
YL	3	2	2	2	0
YS	2	2	1	2	3
LS	2	1	2	3	2
	20	20	12	23	15

VITA 2

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