

GENETIC AND PHENOTYPIC RELATIONSHIPS  
AMONG FIFTEEN MEASURES OF REPRODUCTION  
IN DAIRY CATTLE

by

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Dairy Science

(ABSTRACT)

Reproductive data from 30 research herds were on 31,132 breeding periods of 11,347 dairy cows. Cows were sired by 1,101 sires and had 66,184 services to 1,320 service sires. Several measures of reproductive performance were calculated. These included conception rate, number of services, service period length, days open, age at first breeding, calving interval, days between services, and return to estrus lag. First, second and third service period were each analyzed separately, while fourth and later service periods were pooled.

Heritability was estimated using the sire component of variance and the estimate of the total variance derived from MIVQUEO and maximum likelihood analyses. The data set was restricted to daughters of sires used in multiple herds. Heritability estimates were less than .07 for all traits in the heifer service period except age at first breeding (.2 by maximum likelihood and .13 by MIVQUEO).

Similarly with the exception of conception rate, none of the measures of reproduction had heritabilities greater than .05 for all three remaining service period groups. Conception rate measured as a trait of the male (service sire) ranged from .08 to .135 for second and third service period. Conception rate as female trait (sire) had heritabilities ranging from .09 to .249 for second and third service period.

Low heritability estimates obtained in this and other studies suggest that large progeny or service sire groups will be necessary to identify the small genetic differences between bulls.

Many genetic and phenotypic correlations were forced positive due to a part-whole relationship or due to the fact they were simply different bounds for the same measure. A few correlations were in the range from .50 to .90, but many were not significantly different from zero due to large approximate standard errors.

Repeatabilities based upon pairwise comparisons were in the range from 0 to .13. Repeatabilities for reproductive performance of virgin heifers with first parity ranged from .01 to .06 and were generally smaller than later parities. Repeatabilities based upon repeated measures on the same cow ranged from 0 to .12.

Predicted Differences for female (sire) and male (service sire) reproduction were calculated by Best Linear Unbiased Prediction. This analysis included 207 bulls which were in the data both as sire and service sire. Correlations between proofs for male and female reproduction ranged from  $-.13$  to  $.13$ . These results suggest limited genetic relationships between male and female fertility.

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## TABLE OF CONTENTS

	<u>Page</u>
ABSTRACT . . . . .	ii
ACKNOWLEDGEMENTS . . . . .	v
LIST OF TABLES . . . . .	ix
LIST OF FIGURES . . . . .	xii
 <u>Chapter</u>	
I. INTRODUCTION . . . . .	1
II. LITERATURE REVIEW . . . . .	4
Reasons for Disposal . . . . .	5
Economic Importance of Reproduction . . . . .	5
Inheritance of Reproductive Measures . . . . .	6
Increased Accuracy of Genetic Estimates . . . . .	16
Heifer Reproduction . . . . .	18
Summary of Literature Review . . . . .	21
III. MATERIALS AND METHODS . . . . .	23
Source of Data . . . . .	23
Measures of Reproduction . . . . .	27
Methods of Analysis . . . . .	33
Repeatability of Reproductive Measures . . . . .	37
Genetic Correlation Between Male and Female Reproduction . . . . .	39
IV. RESULTS AND DISCUSSION . . . . .	41
Means and Standard Deviations . . . . .	41
Estimation of Genetic and Phenotypic Parameters . . . . .	43
Heritability Estimates . . . . .	43
Genetic and Phenotypic Correlations . . . . .	46
Repeatabilities . . . . .	53
Pairwise Repeatabilities of Measures of Reproductive Performance . . . . .	53
Repeatability of Measures of Reproductive Performance . . . . .	55

<u>Chapter</u>	<u>Page</u>
Genetic Relationship Between Male and Female Reproduction . . . . .	55
Heifer Reproduction . . . . .	60
V. SUMMARY AND CONCLUSIONS . . . . .	70
BIBLIOGRAPHY . . . . .	74
APPENDIX . . . . .	81
VITA . . . . .	86



LIST OF TABLES

	<u>Page</u>
Table 1. Heritability of Calving Interval (CI), Service Period (SP), and Services/Conception reported by several researchers . . . . .	9
Table 2. Heritability of % Non-Return, % Non-Return Male and Female Fertility reported by several researchers . . . . .	12
Table 3. Heritability of % 60-90 Day Non-Return, and NR Rate reported by several researchers . . . . .	13
Table 4. Heritability of Conception Rate First Service, Male and Female, reported by several researchers . . . . .	15
Table 5. Heritability of Days Open, Days from Calving to first insemination, Days between service (DBS), and age at first and successful breeding reported by several researchers . . . . .	17
Table 6. Estimated heritabilities for non-return rate based on various numbers of inseminations . . . . .	19
Table 7. Herd number, location, frequency, and mean service per conception (S/C) . . . . .	24
Table 8. Records per service period across thirty herds . . . . .	25
Table 9. Characteristics of data set . . . . .	26
Table 10. Abbreviations and descriptions for measures of reproduction . . . . .	28
Table 11. Means and standard deviations for measures of reproductive performance in cows . . . . .	42
Table 12. Heritability estimates by parity from MIVQUEO . . . . .	44
Table 13. Heritability estimates by parity from maximum likelihood (ML) . . . . .	45

	<u>Page</u>
Table 14. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for first parity . . . . .	47
Table 15. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for second parity . . . . .	48
Table 16. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for third and later parity . . . . .	49
Table 17. Approximate standard errors of genetic correlations of reproductive measures for first parity . . . . .	50
Table 18. Approximate standard errors of genetic correlations of reproductive measures for second parity (above diagonal) and third and later parity (below diagonal) . . . . .	51
Table 19. Pairwise repeatabilities of measures of reproduction . . . . .	54
Table 20. Repeatability of measures of reproductive performance . . . . .	56
Table 21. Within trait and gestation correlations between predicted differences for sire and service sire for CRA, CRF, and DBS . . . . .	57
Table 22. Means and standard deviations for measures of heifer reproduction . . . . .	59
Table 23. Heritability estimates for heifer reproduction by maximum likelihood (ML) and MIVQUE0 . . . . .	62
Table 24. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for heifers . . . . .	63
Table 25. Approximate standard errors of genetic correlations of reproductive measures for heifer reproduction . . . . .	64

	<u>Page</u>
Table 26. Genetic correlations for heifer reproduction and first parity reproduction . . . . .	66
Table 27. Approximate standard errors of genetic correlation for heifer reproduction and first parity reproduction . . . . .	67
Table 28. Phenotypic correlations for heifer reproduction and first parity reproduction . . . . .	68

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Interval measures of reproductive performance . . . . .	29
2. Relationship between male and female reproduction . . . . .	58

## Chapter I

### INTRODUCTION

A primary goal of dairy cattle breeding is to develop more profitable cows. Since the early sixties, endeavors to increase milk yield have been successful. Increased yield per cow is partly the result of improved nutrition and herd management, but it is also partially the result of genetic improvement.

The economic importance of reproduction has been well documented. Burnside (10) indicated the primary reason for disposal among Canadian cattle (.21) was breeding problems. Janson (33) reported nearly .30 of all cows culled by Swedish dairymen were due to reproductive disorders.

Research regarding the degree of inheritance of measures of reproduction in dairy cattle has largely centered on differences among cows. This research has been voluminous and has been virtually unanimous in indicating that genetic differences account for less than 10% of this observed variation (18, 26, 27, 32, 41, 64).

Through the use of large numbers of daughter production records, it has been shown that the accuracy of selection among bulls for milk yield can be increased to near unity, in spite of a heritability of individual daughter records

of only .20-.25. Janson (34) suggested despite the low heritabilities, progeny testing of bulls permits evaluation of bulls for reproductive performance of their daughters. Philipsson (64) stated that past conclusions concerning possibility of genetic progress in reproduction had been derived by simply examining heritability of a single record. Philipsson further stated that in populations where selection was based primarily on progeny tests, conclusions should depend on the expected accuracy of sire evaluation instead of heritability estimates which apply only to mass selection.

Genetic improvement for any trait depends upon the selection practices as well as heritability of the trait. Little intentional selection has been placed upon improved reproduction. Some researchers argue that only fertile females reproduce; therefore, natural selection keeps reproductive deterioration at bay. Others suggest that natural selection has left very little genetic variation for reproductive performance and that selection for improved reproduction would yield little if any genetic progress.

The various observed values of reproduction for each cow will be referred to as "measures" rather than the customary traits, since many of the observed values may actually be different measures of the same trait.

The objectives of this study are to determine the heritability, repeatability, and genetic and phenotypic correlations of various measures of reproduction in dairy cattle and to determine the genetic correlation among measures of male and female reproduction.

## Chapter II

### LITERATURE REVIEW

The economic importance of reproduction has been well documented (10, 22, 30, 38, 45, 53). Efficient reproductive performance is necessary to reduce the cost of production. Reproductive problems have long been a major reason for removing cows from dairy herds (20, 87). Cow fertility is singled out by many dairymen as their number one herd problem, even in cases where there is no known infectious disease problem. Thus, other aspects of management appear to be involved. Management practices have changed, and some of these changes may affect breeding efficiency adversely. Some of these changes are: increases in herd size, cows per man, genetic ability of cows, amounts fed, as well as, new housing systems. Many of these changes were made without considering their effects on reproduction or workability in breeding management practices.

Several symposia have dealt with this subject. Areas covered include: 1) estrus detection (23); 2) effect of intensified dairy operation on post-partum reproduction (86); 3) influence of environment on reproduction (82); 4) use of reproduction records (15, 89); 5) influence of estrus detection on days open (5); 6) reproductive management programs (36, 43); and 7) early post-partum breeding (8, 84).



## 2.1 REASONS FOR DISPOSAL

Burnside et al. (10) indicated that either low milk production yield or fertility problems were the major cause of voluntary culling of Canadian Holsteins. Approximately .21 of all disposals were related to breeding problems while only .155 were due to low yield. Surveys of dairy cattle enrolled in Dairy Herd Improvement Associations (DHIA) (1) show that sterility is the second most frequent cause of culling. While animals culled for fertility are not completely sterile, apparently their owners decided they were no longer profitable. O'Bleness and Van Vleck (58) reported that .16 of all cattle in New York were disposed of due to fertility problems. Janson (33) reported that nearly .30 of all cows culled by Swedish dairymen were due to fertility disorders.

## 2.2 ECONOMIC IMPORTANCE OF REPRODUCTION

The reproductive performance of A.I. sires used is an important factor affecting profitability. Everett (22) reported that a dairyman could sacrifice up to 256 pounds of milk to get a .10 increase in the proportion conceived for direct service on bulls selling for \$20 per first service. In another study, McGilliard (53) calculated the influence of conception rate of bulls on the profitability of a dairy enterprise over a 10-year period. His results indicated bulls with zero predicted difference (PD) for

milk and .60 conception rates were as profitable as bulls with PD values of 803 kg. of milk and conception rates of .50. In addition A.I. units report nearly .33 of all culling of dairy bulls from A.I. units in the United States is due to low conception (38).

Maijala (45) listed nine ways in which poor fertility influences the profitability of a dairy: 1) longer calving intervals, 2) increased veterinary expenses, 3) additional breeding costs, 4) more replacements needed, 5) lower average yield due to a higher percentage of young cows in herd, 6) greater feedstuff requirements to grow replacements, 7) less definite time period of subsequent calving, 8) fewer offspring for beef production, and 9) fewer offspring that can be merchandized.

In view of the great economic importance of reproduction to dairymen, it is vital that genetic differences among artificial insemination (A.I.) sires for both male and female reproductive measures be investigated.

### 2.3 INHERITANCE OF REPRODUCTIVE MEASURES

Estimates of the degree of inheritance of measures of reproduction in dairy cattle have largely centered on differences between cows. This research has been voluminous and has been virtually unanimous in indicating that genetic differences account for less than 10% of the observed variations (18, 26, 27, 32, 41, 64).

Low reproductive efficiency due either to delayed first service, missed estrus, or multiple services per conception continues to be a major problem in dairy herds. The greatest variation from one herd to another in days open, calving to first estrus, calving to first service, and therefore, calving interval has been attributed to differences in practices for detection of estrus. Many factors have been implicated in lengthened calving intervals, these include: conception rate, high milk production, seasonal and environmental factors, age of the cow, service sire and others.

The association between the interval from calving to the first service and the number of services per conception has been investigated by a number of researchers (12, 19, 20, 40, 60, 74). In general, these workers reported that the services required per conception decreased as the days from parturition to first breeding increased to 100-120 days, when the number of services per conception reached a minimum.

Maijala (45) reviewed repeatability and heritability estimates of number of services per conception and calving interval for studies from 1931 to 1957. Weighted average of these estimates were .077 (repeatability) and .032

(heritability) for number of services, and .123 (repeatability) and .033 (heritability) for calving interval.

Heritability estimates for calving interval, services per conception and service period as reported by several researchers are summarized in Table 1. Heritability estimates reported in the literature, were based on large data sets, were generally reported to be less than .07 for calving interval, services per conception and service period.

The most frequently used measure of male fertility is rate of non-return to service within some time following first service. There is considerable historical evidence, based on research in the days before the advent of frozen semen, that the repeatability of mean non-return rate is moderate to high, when the performance of bulls is compared across time (9, 52, 66, 75). While these estimates vary according to the traits studied and the time intervals in which reproductive performance was measured, the accuracy is sufficient to cull the worst individual bulls before future A.I. use. The problem that arises is that most studs have only limited data on non-return and the reliability and usefulness of the data is not always known.

Table 1. Heritability of Calving Interval (CI), Service Period (SP), and Services/Conception reported by several researchers.

Trait	Heritability	Number in Study	Source	
Calving Interval (CI)	.005	24,159 heifers, 104 sires	Janson (1980) (34)	
	.096	14,625 Red Danish heifers	Hansen (1978) (31)	
	.03	11,851 Danish Friesian heifers	Hansen (1978) (31)	
	.037		Maijala (1978) (51)	
	.08	551 cows	Zavertyzev and Gordilov (1975) (90)	
	.008	358 daughters of 4 bulls	Rognoni et al. (1965) (67)	
	.324	623 cows (all lactations)	Wilcox and Pjau (1954) (88)	
	.00	1,015 daughters of 52 bulls in 297 herds	Dunbar and Henderson (1953) (18)	
	.10	10,907 Holstein recrods in one herd	Everett et al. (1966) (21)	
	.00	1,016 cows, 2,419 calving intervals	Legates (1954) (41)	
	.02	100,280 cows DHIA Data	Miller et al. (1967) (56)	
	Service Period (SP)	.07	10,907 Holstein records in one herd	Everett et al. (1966) (21)
		.00		Johnson and Everson (1966) (35)
.07		834 cows	Pou et al. (1953) (65)	
.017		17,873 heifers, 96 sires	Janson (1980) (34)	

Table 1 continued

Trait	Heritability	Number in Study	Source
Services/Conception	.08	1,943 cows in 545 herds	Metz and Politiek (1970) (55)
	.24	534 daughters of 9 bulls	Rognoni et al. (1965) (67)
	.00	763 cows	Carmen (1955) (11)
	.26	1,129 cows, 2,443 calvings	Legates (1954) (41)
	.097	381 cows, 15 sires	Branton et al. (1956) (7)
	.05	10,907 Holstein records in one herd	Everett et al. (1966) (21)
	.00		Johnson and Everson (1966) (35)
	.07	834 cows	Pou et al. (1953) (65)
	.013		Olds et al. (1949) (59)
	.03		Maijala (1978) (51)
	.013	24,159 heifers, 104 sires	Janson (1980) (34)
	.017	19,873 heifers, 96 sires	Janson (1980) (34)
	Services/Conception (female fertility)	.013	100,981 inseminations (heifers) 283 sires
.017		81,750 inseminations (first calf) 222 sires	Chavaz and Gaillard (1982) (13)
Services/Conception (male fertility)	.021	125,355 inseminations (heifers) 378 sires	Chavaz and Gaillard (1982) (13)
	.020	117,553 inseminations (first calf) 399 sires	Chavaz and Gaillard (1982) (13)

Shannon and Searle (75) determined the relationship between mean non-return rate of mates for 75 sire-son pairs in New Zealand. This data, based on the use of fresh semen for insemination, included an average of 1,792 and 376 inseminations for sire and son, respectively. Based on the regression of son on sire, the heritability of non-return to first service in 49 days was estimated to be  $.55 + .26$ . These workers also estimated the year to year repeatability of non-return rate to be  $.69 + .05$ , from a total of 314 sires. A summary of heritability estimates for non-return rates are reported in Tables 2 and 3. Heritability estimates vary greatly depending upon the type of non-return rate estimates used (60-90 day or annual non-return).

Selection can be practiced on non-return rates based on heifers with little negative effect on generation interval as the information would be available prior to the decision on the bull's production proof. However, the actual heritability based on the average of larger progeny groups, did not increase as much as the theoretical estimate (Maijala, 46, 48, 50). It was difficult to reach a repeatability of .5 in practice. Maijala (50) also stated that it was very important to eliminate the most important external factors, since even a small increase in heritability at the vicinity of zero decreases considerably the number of daughters required.

Table 2. Heritability of % Non-Return, % Non-Return Male and Female Fertility reported by several researchers.

Trait	Heritability	Number in Study	Source
% Non-Return	.007	6 million inseminations	Murray et al. (1977) (57)
	.06	Stud 1 (Badger) 1,117 records from 34 sires	Collins et al. (1962) (14)
	.08	Stud 2 (Tri-State) 1,097 records from 32 sires	Collins et al. (1962) (14)
	.006	Based on young unselected Holstein bulls	Stocker (1976) (77)
	.004	1,015 cows by 52 bulls in 297 herds	Dunbar and Henderson (1953) (18)
	.04	554 first calf heifers by 29 sires	Rottensten and Touchberry (1957) (68)
% Non-Return (female fertility)			
% NR 1-17 Days	.043	100,981 inseminations (heifer) 283 sires	Chavaz and Gaillard (1982) (13)
	.008	81,750 inseminations (first calf) 222 sires	Chavaz and Gaillard (1982) (13)
% NR 18-24 Days	.019	100,981 inseminations (heifer) 283 sires	Chavaz and Gaillard (1982) (13)
	.013	81,750 inseminations (first calf) 222 sires	Chavaz and Gaillard (1982) (13)
% NR 25-30 Days	.026	100,981 inseminations (heifer) 283 sires	Chavaz and Gaillard (1982) (13)
	.000	81,750 inseminations (first calf) 222 sires	Chavaz and Gaillard (1982) (13)
% Non-Return (male fertility)			
% NR 1-17 Days	.009	125,355 inseminations (heifer) 378 sires	Chavaz and Gaillard (1982) (13)
	.000	117,553 inseminations (first calf) 399 sires	Chavaz and Gaillard (1982) (13)
% NR 18-24 Days	.037	125,355 inseminations (heifer) 378 sires	Chavaz and Gaillard (1982) (13)
	.037	117,553 inseminations (first calf) 399 sires	Chavaz and Gaillard (1982) (13)
% NR 25-30 Days	.013	125,355 inseminations (heifer) 378 sires	Chavaz and Gaillard (1982) (13)
	.012	117,553 inseminations (first calf) 399 sires	Chavaz and Gaillard (1982) (13)



Table 3. Heritability of  $\frac{1}{2}$  60-90 Day Non-Return, and NR Rate reported by several researchers.

Trait	Heritability	Number in Study	Source
$\frac{1}{2}$ 60-90 Day Non-Return	.21	68 sires/274 sons	Gaunt et al. (1976) (24)
	.22	46 sires/252 sons	Gaunt et al. (1976) (24)
	.24	39 sires/161 sons	Gaunt et al. (1976) (24)
	.29	13 sires/172 sons	Stemmler et al. (1973) (78)
	.25	30 sires with at least 4 sons/sire	Murray et al. (1983) (57)
NR Rate 49 day	.55	75 sire-son pairs	Shannon and Searle (1961) (75)
NR Rate (annual)	.35		Maijala (1967) (47)
	.30	49 sires/176 sons	Rendel and Venge (1961) (66)
	.19	83 sires/271 sons	Zelfel (1964) (91)
	.18	839 sires	Maijala (1969) (48)
	.59	39 sires	Samoiilo (1974) (70)
	.10	286 sires	Schmid (1974) (73)
	.20	126 sires	Schmid (1974) (73)
	.39	200 sires	Menendes Buxadera et al. (1978) (54)

Non-return rate is known to overestimate true rate of conception (25, 61, 63) and to be biased by several non-genetic factors (24, 61). Unpublished results from one U.S. breeding organization indicate non-return rates to be systematically lower, 1) for matings in milk recorded herds or in herds of registered animals, 2) for higher percentages of matings to cows, as opposed to heifers, 3) for bulls with superior genetic evaluations for milk yield, 4) for bulls whose semen is more expensive, and 5) for bulls whose semen is special-ordered from other breeding organizations (85). In addition, discarding certain ejaculates and altering numbers of viable sperm tend to mask differences among bulls for conception rate, although seldom if ever, are efforts to remove differences entirely successful (62, 80). These results suggest that meaningful comparisons for non-return can be made only from randomly distributed semen of young bulls in sampling programs, or where adjustments are made for the non-random distribution of semen from bulls (24, 61).

Conception rates can be expressed as a function of male fertility (effect of service sire) or as a function of female fertility (effect of sire of cow). Estimates (summarized in Table 4) for both male and female conception rates varied greatly between researchers but generally

Table 4. Heritability of Conception Rate First Service, Male and Female, reported by several researchers.

Trait	Heritability	Number in Study	Source
Conception Rate First Service (Female)	.021	38 heifers	Bar-Anan et al. (1979) (2)
	.035		Bar-Anan et al. (1980) (4)
	.024	137 cows	Bar-Anan et al. (1979) (2)
	.54	53 sire-son pairs	Siratskii et al. (1974) (76)
	.405	14 sires/37 sons	Trofimenko and Sharapa (1973) (83)
	.156	20 sires	Trofimenko and Sharapa (1973) (83)
	.203	81 sires (half-sib)	Samoilo (1969) (69)
	.264	39 pairs (sire-son)	Samoilo (1969) (69)
Conception Rate First Service (Male)	.034	10 heifers	Bar-Anan et al. (1979) (2)
	.024	32 cows	Bar-Anan et al. (1979) (2)
	.09	738 cows	Zavertyaev and Gordilov (1975) (90)
	.22	? daughters of 43 sires	Dearborn (1970) (16)
	.30	953 cows	Leinbenburg and Bruckner (1970) (42)
	.00	1,000 herds	Hahn (1969) (26)
	.01	500,000 first services	Maijala (1964) (45)
	.00	2,470 cows	Collins et al. (1962) (14)
	.085	1,406 females in 41 herds	Inskeep et al. (1961) (32)
	.004	1,036 cows	Dunbar and Henderson (1953) (18)

those studies based upon upon large numbers of observations estimate the heritability of conception rate for both male and female to be less than .05.

Table 5 contains heritability estimates for five additional measures of reproductive performance. These five measures are days open, days from parturition to first breeding, days between successive inseminations, and two measures of heifer reproductive performance (age at first breeding and age at successful breeding) both expressed in months. Each has heritability estimates of less than .10 and is generally not significantly different from zero, with the exception of age at successful breeding (.156).

#### 2.4 INCREASED ACCURACY OF GENETIC ESTIMATES

Virtually all investigators have ignored the opportunity to generate more accurate estimates of genetic differences in reproductive measures which may be possible through A.I. Through the use of large numbers of daughters production records it has been shown that the accuracy of selection among bulls for milk yield can rise to near unity, in spite of a heritability of individual daughter records of only .20-.25. This is the advantage of A.I.; large numbers of daughters per sire, in many different herd environments, produced from a wide sample of mates. Perhaps a similar procedure could be used to obtain more accurate estimates of genetic differences in reproductive measures.

Table 5. Heritability of Days Open, Days from Calving to first insemination, Days between service (DBS), and age at first and successful breeding reported by several researchers.

Trait	Heritability	Number in Study	Source
Days Open	.05	5,802 cows paternal half-rib	Seykora and McDaniel (1983) (72)
	.13	5,802 cows daughter-dam	Seykora and McDaniel (1983) (72)
	.06	4,539 cows	Krageland et al. (1979) (37)
	.03	72,187 records	Berger et al. (1981) (6)
	.09	4,385 lactations, 9 herds, (all lactation included)	Smith and Legates (1962) (77)
Days Open (150 max.)	.031	41,710 1st parity records	Hansen (1983) (29)
Days Open (305 max.)	.023	41,710 1st parity records	Hansen (1983) (29)
Days from calving to first insemination	.04	72,187 1st lactation records	Berger et al. (1981) (6)
	.03	72,187 2nd, 3rd and later lactation records	Berger et al. (1981) (6)
	.03	41,710 1st and 22,389 3rd lactation records	Hansen et al. (1983) (29)
	.017	31,162 2nd lactation records	Hansen et al. (1983) (29)
	.022	31,263 records (all lactations)	Janson (1980) (34)
Days Between Service (DBS)	.008	22,664 heifer records	Hansen (1983) (29)
Age at Successful Breeding	.156	22,664 heifer records	Hansen (1983) (30)
Age at First Breeding	.060	22,664 heifer records	Hansen (1983) (30)

Past conclusions concerning the possibility of genetic improvement in reproductive traits have been derived by simply examining the heritability of a single record (64). Where selection is on progeny test, sire evaluation is more critical than the heritability of the trait (64). However, despite the low heritabilities, progeny testing of bulls permits the evaluation of bulls based on their daughter's fertility.

A limited number of studies have been devoted to the usefulness and reliability of reproductive data of bulls, based on their A.I. performance. Syrstad (81) calculated the heritability of the average non-return rate based on increasing number of inseminations (Table 6). For the purpose of illustration, he used heritabilities of .005 and .007 and a repeatability of .01, for the outcome of a single insemination. It can be seen that even with a heritability as low as .005 for single insemination, the heritability of average non-return rate reaches .4 at as few as 400 inseminations, which is the minimum required to obtain an adequate number of daughters in a milk production proof.

## 2.5 HEIFER REPRODUCTION

Maijala (45) was the first to postulate that heifer reproductive performance and cow reproductive performance may be essentially unrelated. Hahn (26) reported higher

Table 6. Estimated heritabilities for non-return rate based on various numbers of inseminations.

Number of inseminations	<u>Heritability of non-return rate</u>	
	$h^2 = .005$	$h^2 = .007$
100	.25	.35
200	.33	.47
400	.40	.58
1,000	.45	.64
$\infty$	.50	.70

heritability estimates for heifers than for cows. Thus, he postulated that selection for heifer reproduction may be better than selection for cow reproduction. Hansen (29) reported heritabilities for measures of reproduction in lactating cows to be from zero to .03. In heifers he reported heritabilities from .001 to .156.

Inskeep (32) and Metz and Politics (55) concluded from their data that reproduction measured in lactating cows may be appreciably influenced by genes different than those influencing the reproductive performance in virgin heifers which agrees with Maijala (51). Chavaz and Gaillard (13) using Swiss Simmental cattle measured percent return to service using differing number of days from 1-17 days to 25-30 days. They measured this trait both as an effect of the male (service sire) and of an effect of the female (sire of the cow). Measures of female reproductive performance showed heritability of heifer reproductive performance generally to be higher than for first calf cows. When measured as male reproductive performance, the heritabilities were generally higher than for female reproductive performance, but no conclusions could be drawn between parities (Table 2).

Jansen (34) estimated genetic correlations between reproductive performance of heifer and cow. Correlations between heifer and cow for the same reproductive measure



were between .8 and .9. He concluded from these studies using two separate data sets that generally the same genes controlled heifer and cow reproduction. However, the phenotypic correlations between heifer and first lactation reproductive performance were nearly zero and ranged from -.05 to .05 for 12,179 Swedish cattle.

## 2.6 SUMMARY OF LITERATURE REVIEW

Fertility along with low production has been shown to be a major reason for disposal of dairy cattle, and therefore, is of major economic importance.

Estimates of the degree of inheritance of measures of fertility have almost unanimously been reported to be small. Most studies have reported heritabilities of reproduction measures to be less than .05. Therefore, little response would be expected from mass selection for reproduction.

Several studies have examined the usefulness and reliability of reproduction data of bulls based on their A.I. performance. These researchers have suggested that the accuracy of selection on progeny test is more critical than heritability of a single observation.

Studies conducted between virgin heifers and their relationship with first and later lactation cow reproductive performance have been nonconclusive due to conflicting reports in the literature. In general, higher heritability estimates were reported for measures of heifer reproduction than for cow reproduction.

## Chapter III

### MATERIALS AND METHODS

#### 3.1 SOURCE OF DATA

Reproductive data from thirty research herds across the United States were assembled by Dr. R. H. Miller, Chief of the USDA-ARS, Milk Secretion and Mastitis Laboratory, USDA, Beltsville, Maryland. These herds varied greatly in size, management schemes and location (Table 7). The data covered the years from 1959 to 1977.

The data set contained a total of 31,132 breeding periods on 11,347 animals. Records per service period are presented in Table 8. Animals were sired by 1,101 sires and had 66,184 services from 1,320 service sires. The frequency of herds per sire, herds per service sire (SS), daughters per sire, and services per service sire (SS) are presented in Table 9.

Heifer, first, and second parities were analyzed separately, third and later parities were pooled for all analysis. Sires within each parity group were required to have daughters in more than one herd. Service sires were required to have at least four services in more than one herd to be included. Requiring sires and service sires to be in more than one herd tends to reduce sampling errors and sire and herd confounding.

Table 7. Herd number, location, frequency, and mean service per conception (S/C).

Herd	location	freq.	mean S/C
1	Ohio	1,343	1.51
2	Ohio	458	1.36
3	Ohio	573	1.54
9	Maryland	1,015	1.88
10	Maryland	1,258	1.90
11	Beltsville	3,275	2.21
12	Iowa	793	2.23
13	Iowa	878	2.15
14	Utah	2,821	2.01
15	Minnesota	579	1.71
16	Minnesota	492	1.93
17	Minnesota	827	1.90
21	Arkansas	243	2.38
22	Florida	1,038	2.92
23	Jeanerette	476	1.84
24	Wisconsin	1,223	1.74
30	Baton Rouge	1,641	2.78
32	BYU	2,869	2.56
33	Illinois	1,979	1.97
41	North Carolina	434	1.85
43	North Carolina	913	2.27
45	North Carolina	1,103	2.22
46	North Carolina	930	2.05
47	North Carolina	895	2.70
49	North Carolina	656	2.43
51	Virginia	690	2.07
52	Virginia	717	2.29
53	Virginia	487	2.87
55	Virginia	113	1.72
56	Virginia	413	2.06
TOTAL		31,132	$\bar{X}=2.15$

Table 8. Records per service period across thirty herds.

---

<u>Records per services period</u>	
<u>Service Period<sup>a</sup></u>	<u>Records</u>
0	7,402
1	8,625
2	6,285
3	3,989
4	2,279
5	1,256
6	659
7	304
8	179
9	<u>154</u>
	31,132

---

- <sup>a</sup> 0 = Heifer  
 1-7 = Lactation number  
 8 = Eight lactations or more  
 9 = Unknown lactation number

Table 9. Characteristics of data set.

<u>Herds/Sire</u>		<u>Herds/SS</u>		<u>Dau/Sire</u>		<u>Services/SS</u>	
<u>Sires</u>	<u># Herds</u>	<u>SS</u>	<u># Herds</u>	<u>Sire</u>	<u># Dau.</u>	<u>SS</u>	<u>#Services</u>
741	1	966	1	774	1-9	343	1
160	2	124	2	327	10	640	2-49
84	3	55	3	143	20	194	50-99
24	4	37	4	38	50	118	100-467
28	5	57	5			<u>25</u>	500-1356
52	6-9	49	6-9			1320	
<u>12</u>	10-21	<u>32</u>	10-21				
1101		1320					

Age restrictions were placed on data included in each parity classification to avoid recording errors. Heifer and later parity groups were classified as follows: heifers were required to be at least 12 months, but less than 28 months at first breeding, first parity limits were 18 and 40 months; second parity limits were 28 and 52 months; and third and later parity were 44 and 180 months.

### 3.2 MEASURES OF REPRODUCTION

Fifteen measures of reproduction were evaluated. The relationship between many of the measures of reproductive performance are presented in Figure 1. Abbreviations and descriptions of these measures are presented in Table 10. Several of these reproductive measures have been evaluated by Hansen et al. (27), Laben et al. (39), Berger et al. (6), and Bar-Anan et al. (3). Three of the traits, number of services, days open, and service period had upper bounds placed upon them. The specific choices for the bounds placed upon these three traits were chosen so that these measures of reproduction would be comparable with those found in previous research. Several other measures of reproduction that had been studied previously were also included in this study. This should provide comparison with estimates from other studies that had used various types of field data.

Table 10. Abbreviations and descriptions for measures of reproduction.

Abbreviation	Description
CRF	Percent conception first service
CRA	Percent conception all services (1/total number of breedings)
FB	First breeding (days from parturition to first breeding)
SP91	Service period (maximum of 91 days)
SP244	Service period ( maximum of 244 days)
DBS	Days between services
EL11	Return to estrus lag (divisor; number of breedings between 11-31 days)
ELNS	Return to estrus lag (divisor; total number of repeat breedings)
NS3	Number of services (maximum of 3)
NS9	Number of services (maximum of 9)
CI	Calving Interval
D0150	Days open (maximum 150 days)
D0305	Days open (maximum 305 days)
AGEFB	Heifer age at first breeding in months
AGESB	Heifer age at successful breeding in months



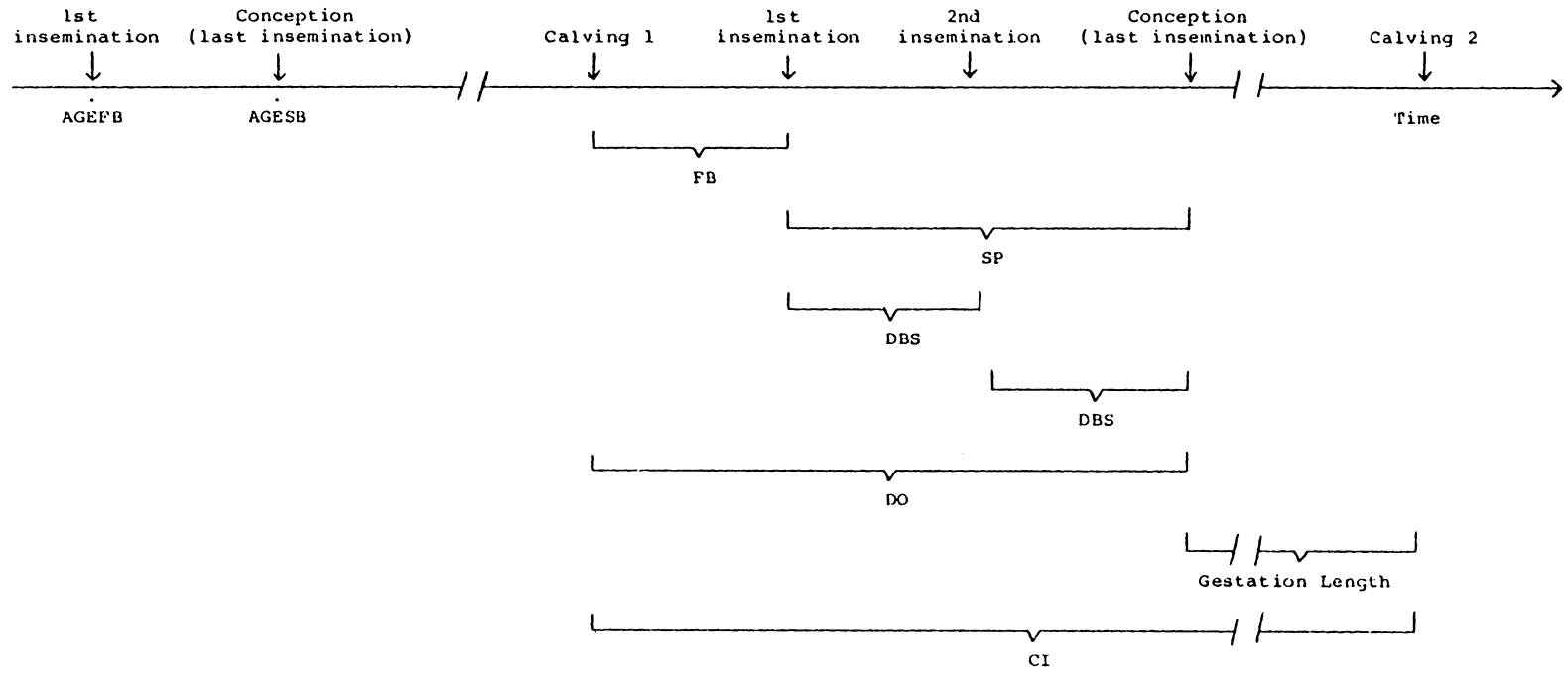


Figure 1. Interval measures of reproductive performance.

Days from parturition to first breeding (FB) have been used by many researchers as one measure of reproductive performance. This is one measure that can be greatly affected by reproductive management of the herd. In addition, any intentional delay of breeding will appear as an environmental effect for that trait. These data were from university or university controlled herds. Thus, the effect of intentional delay of breeding should be minimized but other reproductive management treatments may be present. An upper limit of 305 days was placed on FB (i.e., if  $FB > 305$  then FB set equal to 305) to eliminate uncommonly long periods from calving to first breeding and to make this measure of reproduction comparable with those from previous research. A lower limit was set at 30 days postpartum.

The interval, in days, from first breeding to successful breeding was referred to as service period (SP). Service period also can be affected by management, and therefore, a longer SP to a large extent may represent management differences. Therefore, alternative upper limits were placed on SP, maximum of 91 days SP91 (i.e., if  $SP > 91$  then SP set equal to 91) and 244 days (SP244).

FB and SP sum to days open. Two measures of days open were calculated by setting two upper limits for days open. Maximum days open of 150 days (DO150) allowed for

approximately two breedings after a normal initiation of breeding postpartum and corresponded to SP91. The other upper limit was placed at 305 days (D0305) which allowed for longer days open and corresponded to SP244. Cows that were not checked pregnant in their terminal lactation were assigned the upper limit for service period and days open. No additional services were added to terminal records.

Number of services was also evaluated in this study. Once again, two upper limits were placed on the number of services, maximum of three services (NS3) (i.e., if  $NS3 > 3$  then NS3 set equal to 3) and maximum of nine services (NS9). Nine services was the highest number of services recorded in the data set.

The average interval between consecutive inseminations in dairy cattle is 21 days. Bar-Anan et al. (2) suggested that genetic variation may exist for the rhythm of estrus intervals and for early embryonic death. Bar-Anan et al. (4) reported heritability values of from .06 to .15 for the frequency of return between 22 and 31 days post insemination. Late returns to estrus were presumed to reflect the failure of implantation or early embryonic death. Bar-Anan et al. (4) further suggested the mating sire affected the rate of fertilization and the genetic effect of the cow and her sire affected the rate of implantation of the conceptus.

In the current study, days between services (DBS) and return to estrus lag (EL11 and ELNS) were analyzed. DBS was the interval between successive breedings. If only one breeding was necessary, then DBS was set equal to 21 days. EL11 and ELNS were ratios with numerators equal to the number of repeat breedings in the lactations that were 22 to 31 days after a previous breeding. The denominator of EL11 was the number of rebreedings that were 11 to 31 days after a previous breeding, whereas, the denominator of ELNS was the total number of repeat breedings. If no repeat breedings were necessary, then EL11 and ELNS were set to zero.

Calving Interval (CI) is a result of days open plus gestation length. CI was calculated as the days from previous calving to subsequent calving. If there was no subsequent calving or the subsequent calving was less than 296 days (FB at least 30 days and gestation of at least 266 days) after the previous calving, the observation was deleted.

Conception rate can be used as a measure of both male and female fertility. Two measures of conception rates were used. Conception rate first service (CRF) was defined as one, if a first service resulted in a pregnancy and zero otherwise. Conception rate all services, (CRA) was defined as one over the number of services. CRFM was the first

service conception rate (0 or 1) of the mates of a particular sire. CRFF was the first service conception rate of the daughter of a particular sire. CRAM and CRAF were the percent all service conception rate of mates or daughters of a particular sire. A successful breeding was determined by a pregnancy palpation code or a subsequent calving 266-290 days following last breeding. If a subsequent calving was more than 290 days past last breeding, a new last breeding was assigned by subtracting 278 days from subsequent calving. If gestation length was less than 266 days or no subsequent calving was recorded, the record was deleted.

It was not possible to evaluate FB, CI, D0150, or D0305 for virgin heifers. Age at first breeding (AGEFB) and age at successful breeding (AGESB) were measured in days for all virgin heifer. Successful breeding was determined in the same manor as conception rate.

### 3.3 METHODS OF ANALYSIS

Dairy records are customarily analyzed by accounting for variation due to several fixed effects and coupled with random genetic effects to constitute a mixed model. Janson (33) reported herd and season to be the most important factors affecting reproduction. Often for ease of computation herd, years, and season are combined into a single effect herd-year-season. For the purpose of these

analysis, year and season were combined but not herd. Each year was divided into three equal seasons (January-April, May-August, September-December) to form the year-season variable.

The following model was used to describe female reproductive performance (effect of the sire of the cow).

$$Y_{ijklm} = u + S_i + A_j + YRSN_k + R_1 + b_1 (X_{1,ijklm} - \bar{X}_1) + b_2 (X_{2,ijklm} - \bar{X}_2) + e_{ijklm}$$

where  $Y_{ijklm}$  was the observed fertility measure of the  $m^{\text{th}}$  animal, of the  $i^{\text{th}}$  sire, in the  $j^{\text{th}}$  age class, in the  $k^{\text{th}}$  year-season of first service; in the  $l^{\text{th}}$  class of time to first service:  $u$  was the overall mean,  $S_i$  was the random effect of the  $i^{\text{th}}$  sire;  $A_j$  was the fixed effect of the  $j^{\text{th}}$  age class in months;  $YRSN_k$  was the fixed effect of year-season of first service;  $R_1$  was the fixed effect of class of time to first service in days;  $b_1$  and  $b_2$  were partial regression coefficients,  $X_{1,ijklm}$  was the mean number of services (Table 7) of all animals in the same herd as the  $m^{\text{th}}$  animal in the  $ijkl^{\text{th}}$  subclass;  $X_{2,ijklm}$  was the percent of mates of this animal's service sire which returned to service in 1-75 days ( $R_{1-75}$ ) of those that did not conceive to first service;  $\bar{X}_2$  (overall mean) = .3235; and  $e_{ijklm}$  was the random error, where  $e \sim N(0, \sigma^2_e)$ .

Analyses to determine the effects of male reproductive performance (effect of the mating bull or service sire) used the same model, except  $S_i$  was the random effect of the  $i^{\text{th}}$  mating bull and the regression term of the mating bull was omitted from the model. When heifer reproductive performance was analyzed, the class of time to first service was omitted from the model. In addition, when the measure, days to first breeding was calculated  $R_1$  was omitted from the model. Heifers, first, and second parities were analyzed separately. Third and later parities were pooled for all analysis.

The following Statistical Analysis System (SAS) routines were used to estimate the variance components: 1) General Linear Model (GLM), 2) MIVQUE0, 3) Maximum likelihood (ML) (71). The GLM procedure used the previously mentioned model to estimate the variance components while MIVQUE0 and maximum likelihood (ML) used the following model.

$$Y_{ijklmno} = u + S_i + A_j + YRSN_k + R_l + H_m + MS_n + e_{ijklmno}$$

where  $Y_{ijklmno}$  was a dependent variable (an observed value of a fertility measure),  $u$  was the overall mean,  $S_i$  was the random effect of the  $i^{\text{th}}$  sire,  $A_j$  was the fixed effect of the  $j^{\text{th}}$  age class in months,  $YRSN_k$  was the fixed effect of

year-season of first service,  $R_1$  was the fixed effect of class of time to first service in days,  $H_m$  was the fixed effect of the  $m^{\text{th}}$  herd,  $MS_n$  was the fixed effect of the  $n^{\text{th}}$  mating sire, and  $e_{ijklmno}$  was the random error, where  $e \sim N(0, \sigma^2_e)$ .

Maximum likelihood (ML) selects values for the parameters being considered such that the probability of obtaining the data vector is a maximum. An underlying normal distribution is assumed. ML is constrained to nonnegative estimators and yields sufficient estimators when they exist; however, maximum likelihood estimates may be biased. An iterative procedure was applied that used prior estimates of the components of variance obtained from MIVQUE0 for initialization.

Heritability was estimated as four times the sire component of variance divided by the sum of the sire and error components of variance. Standard errors of heritability, for the GLM procedure, were approximated by methods adapted from Dickerson (17). The heritability estimates and approximate standard errors for the GLM procedure are presented in appendix tables 1 through 4. Standard errors were not calculated for the MIVQUE0 and ML heritability estimates.



The estimates of genetic correlations between measures of reproductive performance were obtained by dividing the sire component of covariance between the two measures by the square root of the product of the sire components of variance for the two measures. An approximate standard error was calculated for each estimate of genetic correlation (17).

The phenotypic correlations between the measures of reproductive performance are Pearson's product moment correlations calculated using the Statistical Analysis System (SAS) routine, procedure correlation.

#### 3.4 REPEATABILITY OF REPRODUCTIVE MEASURES

Repeatability was estimated by two methods. The first method was an intra-class correlation from a mixed model analysis of variance from multiple records on the same individual. Correction factors for age and time were obtained by ordinary least-squares procedures. The following general linear model was used:

$$Y_{ijk} = u + A_i + T_j + e_{ijk}$$

where  $Y_{ijk}$  was a dependent variable (an observed value of a fertility measure),  $u$  was the overall mean,  $A_i$  was the fixed effect of the  $i^{\text{th}}$  parity,  $T_j$  was the fixed effect of the class of time to first service in days, and  $e_{ijk}$  was

the random error, where  $e \sim n(0, \sigma_e^2)$ . These additive correction factors were used to adjust the data. Then a within herd nested analysis of variance, between and within cow, was used to obtain repeatability ( $r$ ) estimates.

The second method of estimating repeatability was a correlation between pairs of observations on the same individual. Repeatability ( $r$ ) estimates were calculated with

$$r = \frac{\text{Cov}(R_1, R_2)}{\sqrt{V(R_1) V(R_2)}}$$

where  $\text{Cov}(R_1, R_2)$  was the covariance between observations, and  $V(R_1)$  and  $V(R_2)$  were the variance of the two records observed on each cow. Cows were not required to have three records to be considered; all parity pairs of observations were involved in repeatability estimation.

Separate analyses were performed for: 1) previous record, 2) the later record, and 3) the sum of two records. The variance of the sum of two variables is

$$V(R_1 + R_2) = V(R_1) + V(R_2) + 2 \text{Cov}(R_1, R_2)$$

where  $V(R_1 + R_2)$  is the variance of the sum of two correlated variables,  $V(R_1)$  and  $V(R_2)$  are the individual variances of the variables, and  $\text{Cov}(R_1, R_2)$  is the

covariance between the two variables. The covariance between observations can be solved for from the individual variances of the variables and the variance of the sum of the two variables.

Repeatabilities included all cow variations of additive genetic, nonadditive genetic, and permanent environment. Therefore, repeatability was considered to be the upper limit of heritability which involved additive genetic variation.

### 3.5 GENETIC CORRELATION BETWEEN MALE AND FEMALE REPRODUCTION

The genetic correlation between the direct or service sire effect and the maternal or sire of the cow effect (Figure 2) was calculated as the correlation between the predicted differences (PD) of a bull, as a sire and service sire, for the same trait.

A best linear unbiased prediction (BLUP) method of analysis was used to calculate the PD for the various reproductive measures. First a PD for the direct effect (male or service sire) of a reproductive measure was calculated and second a PD for the maternal effect (female or sire of the cow) of the same reproductive measure was calculated. The BLUP analysis included the relationship matrix, sire and maternal grandsire, and augmented the sire

diagonal by the variance ratio (error variance/sire variance). The BLUP analysis used an iterative procedure, and for this analysis, the maximum number of iteration was 150, with a convergence criterion of .01.

The correlation between these two different genetic measures for the same reproductive measure was considered to be an approximate genetic correlation between the direct-maternal (male-female) relationship.

## Chapter IV

### RESULTS AND DISCUSSION

#### 4.1 MEANS AND STANDARD DEVIATIONS

Means and standard deviations for various measures of fertility are presented in Table 11. Percent CRF is the average percent conception based upon first services only, while percent CRA is the average percent conception based upon all services. An observation for CRF (conception rate first service) is zero or one based upon pregnancy from first service for the service period of a cow. An observation for CRA (conception rate all services) is one divided by the total number of services for the service period of a cow. For all first services that result in a pregnancy, CRF equals CRA. Means and standard deviations for percent CRA and percent CRF were similar for first and second parities, however, both percent CRA and CRF declined greatly for third and later parities. In addition, the standard deviations were much larger for third and later parities. This lower percent conception is most likely due to a depressing effect of age on fertility.

DBS in the current study agreed closely with Hansen (27) for first and second parities but third and later parities were somewhat longer than Hansen reported. All parities tended to have nearly the same mean and standard deviations

Table 11. Means and standard deviations for measures of reproductive performance in cows.

Measure	<u>Parity 1 (3516)</u>		<u>Parity 2 (2242)</u>		<u>Parity 3 and later (4507)</u>	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
CRA	62.6	33.6	62.5	32.8	45.1	40.4
CRF	43.4	49.5	42.2	49.4	31.4	46.4
NS3	1.9	.90	1.9	.89	2.1	.88
NS9	2.4	1.63	2.3	1.47	2.6	1.92
SP91	20.8	36.5	23.4	35.7	23.6	36.3
SP244	27.6	50.4	29.2	46.2	31.1	52.2
EL11	.22	.38	.26	.41	.28	.42
ELNS	.17	.31	.21	.34	.21	.33
D0150	111.2	32.8	111.1	32.6	108.5	32.9
D0305	124.5	53.2	122.3	50.1	118.4	48.9
FB	81.9	25.0	82.1	25.1	82.7	27.6
CI	402.6	54.0	400.6	50.8	402.4	68.0
DBS	27.7	17.3	27.6	16.8	32.1	25.7

for NS3 and NS9. The NS3 and NS9 means were approximately the same as Berger (6) but somewhat larger than both Janson (34) and Hansen (27). The higher number of services for NS9 may represent the fact that in most of the research herds, project daughters are allowed more services before being culled than a normal dairy herd would allow.

In the current study, SP91 and D0150 were slightly longer than other studies (6, 29, 34), but SP244 and D0305 were much longer. A part whole relationship existed between days open and service period. Thus, D0305 is expected to be longer when SP244 is longer. The longer days open may again be due in part to the greater opportunity that most cows in the data set were given to conceive.

## 4.2 ESTIMATION OF GENETIC AND PHENOTYPIC PARAMETERS

### 4.2.1 Heritability Estimates

Estimates of heritability were calculated using two methods, MIVQUE0 (Table 12) and maximum likelihood (ML) (Table 13). The two methods are in close agreement for most reproductive measures across parity groups.

In general, heritability estimates concur with studies that report heritabilities of reproductive measures to be at or near zero. The exceptions are percent conception rate female CRA, sire which had heritability estimates from

Table 12. Heritability estimates by parity from MIVQUEO.

Measure	Heritability Estimates		
	1st Parity	2nd Parity	3rd <sup>a</sup> Parity
CRF (female)	.065	.133	.006
CRF (male)	.091	.091	.065
CRA (female)	.178	.249	.004
CRA (male)	.089	.135	.012
DBS (female)	.044	.021	.009
DBS (male)	.021	.000	.041
D0150	.023	.028	.000
D0305	.019	.034	.000
NS3	.037	.037	.026
NS9	.046	.017	.041
EL11	.042	.064	.158
ELNS	.052	.036	.140
SP91	.000	--- <sup>a</sup>	.016
SP244	.013	--- <sup>b</sup>	.022
FB	.027	.026	.021
CI	.063	.063	.002

<sup>a</sup>Third and later parities pooled for all analysis.

<sup>b</sup>Negative estimate of  $h^2 = -.003$ .

<sup>c</sup>Negative estimate of  $h^2 = -.019$ .



Table 13. Heritability estimates by parity from maximum likelihood (ML).

Measure	Heritability Estimates		
	1st Parity	2nd Parity	3rd <sup>a</sup> Parity
CRF (female)	.048	.108	.008
CRF (male)	.079	.066	.061
CRA (female)	.092	.131	.073
CRA (male)	.078	.099	.092
DBS (female)	.025	.023	.005
DBS (male)	.016	.000	.037
DO150	.007	.018	.000
DO305	.007	.018	.000
NS3	.036	.018	.038
NS9	.035	.003	.061
EL11	.023	.047	.158
ELNS	.022	.036	.143
SP91	.000	.000	.061
SP244	.001	.000	.033
FB	.021	.014	.021
CI	.046	.033	.002

<sup>a</sup>Third and later parities pooled for all analysis

.004 to .249, percent conception rate male (CRA service sire) which had heritability estimates which ranged from .012 to .135 and return to estrus lag (EL11 and ELNS) for third and later parities only (approximately .15). Heritabilities for SP91, SP244, and DBS (male and female) were consistently lowest across all parity groups, whereas, percent conception rate first service male (service sire) generally was the highest across parities. Heritability estimates of EL11 and ELNS were much higher than Hansen (27) but were in general agreement with Bar-Anan (4).

Where two limits were placed on the same measure of reproductive performance, no consistent trend was found. Heritability estimates for the two limits for the same trait and parity tended to be similar. Limiting these measures may have reduced the environmental variation as intended; however, in most cases, the limit caused a proportional decrease in the genetic variation.

#### 4.2.2 Genetic and Phenotypic Correlations

Genetic and phenotypic correlations among the various measures of reproduction are in Tables 14, 15 and 16. The approximate standard errors of the genetic correlations are in Tables 17 and 18. Many of the genetic and phenotypic correlations are forced positive, due to the fact that several of the reproductive measures are simply different

Table 14. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for first parity<sup>a</sup>.

	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>b</sup>
CRA	-	.946	-.979	-.907	-.263	-.209	-.949	-.907	-.825	-.845	.011	-.833	-
CRF	.955	-	-.975	-.783	-.353	-.307	-.913	-.913	-.814	-.805	-.076	-.802	-
NS3	-.969	-.911	-	.827	.311	.275	.928	.849	.804	.805	.018	.794	-
NS9	-.874	-.736	.853	-	.212	.037	.877	.922	.761	.829	-.124	.826	-
EL11	-.523	-.509	.514	.435	-	.945	.279	.253	.297	.281	.142	.325	-
ELNS	-.478	-.484	.455	.375	.946	-	.212	.142	.216	.159	.086	.209	-
SP91	-.909	-.829	.905	.876	.429	.337	-	.951	.881	.915	.082	.902	-
SP244	-.839	-.735	.822	.902	.382	.284	.951	-	.872	.952	.052	.949	-
D0150	-.763	-.707	.761	.719	.364	.293	.827	.775	-	.945	.416	.925	-
D0305	-.731	-.641	.717	.785	.337	.241	.845	.886	.914	-	.356	.982	-
FB	.134	.117	-.128	-.146	-.052	-.059	-.116	-.129	.386	.345	-	.306	-
CI	-.705	-.624	.694	.751	.335	.241	.813	.849	.878	.959	.332	-	-
DBS	-.278	-.337	.255	.142	.031	-.026	.462	.454	.385	.419	-.021	.404	-

<sup>a</sup>Approximate standard errors of genetic correlations are in Table 17.

<sup>b</sup>Negative estimate of genetic variance.

Table 15. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for second parity <sup>a</sup>.

	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>b</sup>
CRA	-	.965	-.961	-.896	-.608	-.554	-.938	-.867	-.907	-.867	-.078	-.871	-
CRF	.949	-	-.951	-.808	-.612	-.531	-.865	-.779	-.869	-.795	-.115	-.799	-
NS3	-.964	-.896	-	.923	.633	.576	.909	.799	.912	.848	.225	.866	-
NS9	-.871	-.729	.863	-	.596	.527	.896	.881	.808	.857	.031	.862	-
EL11	-.553	-.536	.527	.477	-	.911	.576	.508	.583	.463	-.072	.467	-
ELNS	-.496	-.506	.447	.390	.934	-	.502	.366	.522	.311	-.110	.319	-
SP91	-.903	-.814	.898	.874	.442	.323	-	.949	.897	.916	.004	.929	-
SP244	-.836	-.726	.823	.871	.406	.274	.957	-	.793	.925	-.104	.923	-
D0150	-.759	-.694	.755	.716	.391	.301	.826	.778	-	.897	.344	.904	-
D0305	-.718	-.624	.711	.753	.358	.238	.836	.867	.920	-	.282	.998	-
FB	.105	.092	-.097	-.099	-.032	-.028	-.093	-.110	.404	.400	-	.282	-
CI	-.706	-.619	.696	.734	.362	.248	.819	.843	.901	.971	.386	-	-
DBS	-.301	-.350	.265	.153	.207	-.040	.483	.494	.401	.438	-.035	.429	-

<sup>a</sup>Approximate standard error of genetic correlations are in Table 18.

<sup>b</sup>Negative estimate of genetic variance.

Table 16. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for third and later parity<sup>a</sup>.

	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>b</sup>
CRA	-	.925	-.966	-.933	-.645	-.572	-.855	-.849	-.628	-.849	.100	-.629	-
CRF	.897	-	-.901	-.780	-.533	-.529	-.890	-.848	-.717	-.665	.024	-.696	-
NS3	-.689	-.734	-	.908	.585	.557	.871	.836	.537	.454	-.126	.509	-
NS9	-.613	-.546	.814	-	.627	.566	.715	.716	.366	.355	-.242	.404	-
EL11	-.426	-.448	.575	.505	-	.939	.576	.551	.363	.337	-.018	.219	-
ELNS	-.352	-.414	.475	.379	.919	-	.552	.289	.347	.289	.046	.215	-
SP91	-.454	-.511	.617	.442	.323	.259	-	.700	.723	.657	.007	.726	-
SP244	-.378	-.413	.522	.409	.273	.211	.926	-	.662	.692	-.043	.352	-
D0150	-.353	-.420	.416	.273	.216	.175	.567	.478	-	.918	.436	.930	-
D0305	-.339	-.385	.386	.279	.185	.139	.558	.515	.925	-	.355	.931	-
FB	.359	.071	-.090	-.089	-.061	-.068	-.095	-.105	.300	.273	-	.352	-
CI	-.328	-.351	.398	.359	.158	.084	.319	.273	.534	.553	.263	-	-
DBS	-.145	-.173	.167	.106	.007	-.036	.218	.204	.168	.186	.017	.214	-

<sup>a</sup>Approximate standard errors of genetic correlations are in Table 18.

<sup>b</sup>Negative estimate of genetic variance.

Table 17. Approximate standard errors of genetic correlations of reproductive measures for first parity.

	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>a</sup>
CRA	-	.015	.008	.025	.155	.203	.017	.028	.046	.041	.148	.044	-
CRF		-	.017	.055	.160	.210	.034	.051	.058	.061	.164	.062	-
NS3			-	.037	.152	.199	.022	.037	.049	.048	.151	.051	-
NS9				-	.140	.184	.027	.016	.050	.032	.122	.016	-
EL11					-	.037	.151	.141	.154	.139	.192	.138	-
ELNS						-	.201	.189	.206	.187	.244	.188	-
SP91							-	.012	.032	.024	.146	.027	-
SP244								-	.035	.013	.133	.015	-
D0150									-	.016	.124	.021	-
D0305										-	.115	.004	-
FB											-	.120	-
CI												-	-
DBS													-

<sup>a</sup>Negative estimate of genetic variance.

Table 18. Approximate standard errors of genetic correlations of reproductive measures for second parity (above diagonal) and third and later parity (below diagonal).

	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>a</sup>
CRA	-	.012	.010	.026	.098	.115	.019	.034	.034	.042	.149	.043	-
CRF	.010	-	.021	.053	.105	.124	.039	.057	.049	.062	.158	.064	-
NS3	.030	.032	-	.028	.098	.119	.025	.045	.035	.046	.151	.046	-
NS9	.039	.057	.024	-	.096	.115	.025	.027	.047	.037	.136	.038	-
EL11	.081	.086	.072	.070	-	.027	.103	.108	.108	.116	.162	.118	-
ELNS	.092	.089	.079	.081	.014	-	.125	.133	.128	.140	.174	.141	-
SP91	.059	.047	.039	.063	.080	.085	-	.011	.029	.024	.140	.024	-
SP244	.067	.060	.050	.067	.086	.092	.087	-	.046	.020	.135	.023	-
D0150	.082	.067	.079	.093	.094	.097	.055	.047	-	.023	.125	.024	-
D0305	.083	.072	.084	.092	.094	.099	.061	.061	.016	-	.127	.003	-
FB	.120	.116	.108	.104	.108	.111	.107	.111	.088	.092	-	.129	-
CI	.099	.087	.096	.104	.118	.122	.080	.084	.047	.045	.110	-	-
DBS <sup>a</sup>	0	0	0	0	0	0	0	0	0	0	0	0	-

<sup>a</sup>Negative estimate of genetic variance.

bounds for the same measures, such as SP91 and SP244. With others, the positive correlation may be due to one trait being totally determined by two other traits, such as D0305 which is approximately equal to FB plus SP244.

Some correlations were of interest. In first, second, third and later parities, NS3 and D0150 were genetically correlated .804, .912, and .537 respectively with approximate standard errors of .049, .035, and .079. The genetic correlation for NS3 and CI were .794, .866, and .509 respectively for the three groups measured. The approximate standard errors were .051, .046, and .096 respectively. The extremely high genetic correlation between some of these traits are, in a large part, due to the fact that one measure reflects significantly on the other. An example of that is NS3 and D0150. If a cow is bred the first time at 80 days and is bred three times at 21-day intervals, then the days open would be 143. As can be seen, D0150 and NS3 under this situation would be measuring a similar time period and would expect to have as they do an extremely high genetic correlation. Due to large approximate standard errors, many of the genetic correlations, that were not part-whole relationships, were not significantly different from zero.



### 4.3 REPEATABILITIES

#### 4.3.1. Pairwise Repeatabilities of Measures of Reproduction

Table 19 contains repeatabilities based upon pairwise comparisons. Consecutive parities usually had higher repeatability estimates than first and third parities. Repeatability estimates were less than .09 for all measures of reproductive performance, except FB between parity one and two, which was .125. Repeatabilities between parities two and three were generally higher than between parities one and two. Possibly effects of common environment became relatively greater with an increase in age.

Service period and number of services both had two upper bounds and in every case except one, the larger upper bound had a larger repeatability. Perhaps this was because cows given special treatment in one parity were also given special treatment in later parities.

Repeatabilities for heifer and first parity reproduction were generally smaller than corresponding repeatabilities for older cows. This suggests that permanent environmental effects became greater with older cows. In addition, it might also suggest that heifer and cow fertility may not be closely related. Both Hansen (27) and Maijala (45) reported repeatability estimates in the range of .01-.15 for various reproductive traits. In the current study the

Table 19. Pairwise repeatabilities of measures of reproduction.

Measure	Heifer & Parity 1	Parity 1 & Parity 2	Parity 2 & Parity 3	Parity 1 & Parity 3
CRA	.065	.059	.079	.060
CRF	.046	.039	.063	.034
D0150	-	-.014	-.005	-.099
D0305	-	-.025	-.008	-.089
CI	-	.021	.017	.039
SP91	.038	.018	.066	.051
SP244	.046	.052	.088	.052
NS3	.036	.058	.073	.053
NS9	.038	.033	.085	.055
EL11	.046	.069	.078	.010
ELNS	.036	.063	.053	-.005
FB	-	.124	.043	.028
DBS	.014	.021	.000	-.008

range in estimates were between 0-.12. In general, the repeatability estimates in the current study were slightly larger than those reported by Hansen (27) and Maijala (45), except those for days open.

#### 4.3.2. Repeatability of Measures of Reproductive Performance

Repeatabilities of measures on the same cow, for the various reproductive measures, are presented in Table 20. CRF, CRA and DBS were in the same range as those for pairwise comparisons at .038, .050, and .00 respectively, but CI, D0150, D0305, NS9 and SP244 all had repeatability estimates that were larger than those for the average of the pairwise comparisons at .073, .044, .057, .123, and .119 respectively.

Hansen (28) reported that for those traits where an upper bound was set, the higher bound yielded a higher repeatability estimate. This was also found to be true in the current study. SP244, D0305 and NS9 all had higher repeatability estimates than the lower bound of the respective measures.

#### 4.4 GENETIC RELATIONSHIP BETWEEN MALE AND FEMALE REPRODUCTION

Predicted differences (PD's) for female (sire) and male (service sire) reproductive measures were calculated by best linear unbiased prediction (BLUP), for each gestation separately. The correlations between these two genetic

Table 20. Repeatability of measures of reproductive performance.

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<u>Measure</u>	<u>Repeatability</u>
CI	.073
FB	.092
D0150	.044
D0305	.057
CRF	.038
CRA	.050
NS3	.067
NS9	.123
EL11	.041
ELNS	.036
SP91	.076
SP244	.119
DBS	.00

---

Table 21. Within trait and gestation correlations between predicted differences for sire and service sire for CRA, CRF, and DBS.<sup>a</sup>

Gestation	Direct-maternal correlations		
	CRA <sup>b</sup>	CRF <sup>b</sup>	DBS <sup>b</sup>
0	.039	.077	.034
1	.117*	.128*	.103
2	.027	.049	-.134*
3 <sup>b</sup>	-.091	-.127*	.015

<sup>a</sup>predicted differences based upon 207 bulls which were used in the data as sire and service sire.

<sup>b</sup>Third and later gestations were pooled.

\*Significant at  $P < .10$

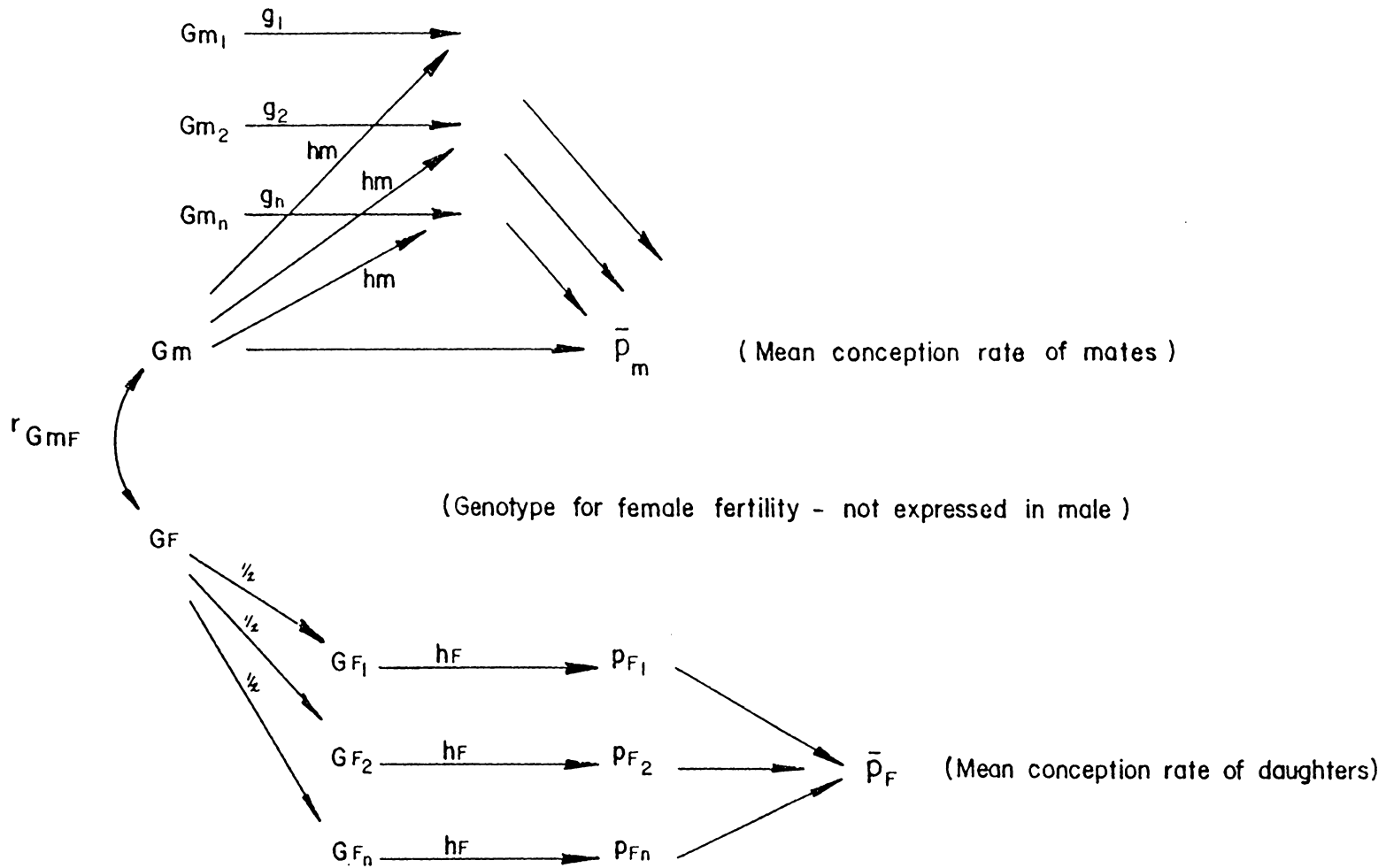


Figure 2. Relationship between male and female fertility.

Table 22. Means and standard deviations for measures of heifer reproduction.

Measure	<u>Heifer Fertility (3735)</u>	
	Mean	SD
CRA	67.9	33.6
CRF	51.6	49.9
NS3	1.8	.9
NS9	2.2	1.7
SP91	31.0	37.1
SP244	43.9	64.0
EL11	.13	.31
ELNS	.10	.25
DBS	29.1	25.1
AGEFB	16.4	2.02
AGESB	17.9	2.89

estimates for male and female measures of the same trait are presented in Table 21 and illustrated in Figure 2. The correlation approximated the genetic correlation between the direct and maternal (male-female) expression for the various reproductive measures.

The direct-maternal correlations were significant for CRA and CRF for gestation one ( $P < .1$ ); for DBS for gestation two; and CRF for third and later gestations. However, correlations between the proofs for male and female for the same traits ranged from  $-.13$  to  $.13$ . These results would suggest limited genetic relationship between male and female reproduction.

#### 4.5 HEIFER REPRODUCTION

Means and standard deviations for heifer reproduction are in Table 22. Compared to the first parity means (Table 11), heifer reproduction was poorer for measures of SP91, SP244, and DBS, while all other means of reproductive measures favored heifers. One possible reason that service period and days between service are longer is that heat detection on heifers may not be as good as on older cows. These results were similar to Hansen (27), except that for AGEFB and AGESB in the current study were 16.4 and 17.9



months while Hansen (27) reported 18.8 and 20.7 months. In addition, CRA and CRF percentages were both slightly higher for heifers, but the standard deviations were almost identical to those reported by Hansen (27).

Heritabilities calculated using MIVQUE0 and maximum likelihood (ML) are presented in Table 23. The two methods were in excellent agreement except for AGEFB where MIVQUE0 estimated heritability to be .099 and the estimate from ML was .219. AGEFB and AGESB had the highest heritability, which agreed with Hansen (27). Therefore, a reasonable response could be anticipated from selection but unlike Hansen, the current study estimated heritability for other measures of heifer reproduction to be generally lower than that of first and later parities.

Genetic and phenotypic correlations of heifer reproduction are in Table 24, with approximate standard errors of genetic correlations in Table 25. The genetic and phenotypic correlations generally agreed with those for the first and later parities, but several were in sharp contrast with those reported by Hansen (27). An example of the contrast is AGESB and AGEFB. Hansen's estimate of phenotypic correlation was almost identical to the current study, but his genetic correlation estimate was  $.966 + .036$  and in the current study the estimate was  $-.06 + .147$ .

Table 23. Heritability estimates for heifer reproduction by maximum likelihood (ML) and MIVQUEO.

Measure	Heritability estimates	
	ML	MIVQUEO
CRF (female)	.004	.004
CRF (male)	.046	.056
CRA (female)	.011	.022
CRA (male)	.044	.051
DBS (female)	.000	-.002
DBS (male)	.018	.023
AGEFB	.219	.099
AGESB	.201	.131
NS3	.005	.012
NS9	.016	.026
EL11	.014	.024
ELNS	.001	.011
SP91	.063	.047
SP244	.066	.044

Table 24. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) of reproductive measures for heifers.<sup>a</sup>

	AGEFB	AGESB	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	DBS <sup>b</sup>
AGEFB	-	-.060	.293	.409	-.273	-.157	.129	.151	-.295	-. <sup>b</sup>	-
AGESB	.632	-	-.760	-.731	.732	.905	.428	.377	.838	.985	-
CRA	.085	-.539	-	.995	-.973	-.911	-.509	-.593	-.945	-.823	-
CRF	.074	-.449	.948	-	-.995	-.919	-.565	-.668	-.954	-.807	-
NS3	-.083	.541	-.971	-.904	-	.883	.543	.646	.921	.782	-
NS9	-.117	.583	-.857	-.712	.844	-	.394	.443	.918	.935	-
EL11	-.004	.222	-.439	-.433	.437	.346	-	.949	.454	.435	-
ELNS	-.002	.135	-.392	-.408	.375	.278	.933	-	.457	.391	-
SP91	-.077	.634	-.908	-.822	.919	.864	.369	.273	-	.888	-
SP244	-.092	.715	-.789	-.667	.787	.872	.298	.184	.903	-	-
DBS	-.017	.393	-.296	-.309	.294	.208	.068	.005	.457	.503	-

<sup>a</sup>Approximate standard errors of genetic correlation are in Table 25.

<sup>b</sup>Negative estimate of genetic variance.

Table 25. Approximate standard errors of genetic correlations of reproductive measures for heifer reproduction.

	AGEFB	AGESB	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	DBS <sup>a</sup>
AGEFB	-	.147	.155	.181	.158	.134	.171	.226	.152	-	-
AGESB		-	.056	.082	.060	.025	.122	.175	.037	.004	-
CRA			-	.012	.008	.026	.117	.156	.019	.045	-
CRF				-	.020	.054	.131	.170	.036	.070	-
NS3					-	.033	.115	.157	.022	.051	-
NS9						-	.112	.155	.024	.018	-
EL11							-	.032	.123	.119	-
ELNS								-	.173	.171	-
SP91									-	.026	-
SP244										-	-
DBS											-

<sup>a</sup>Negative estimate of genetic variance.

Only heifers with confirmed first parity reproductive performance were considered for correlations of heifer and first parity reproduction. Genetic correlations are in Table 26 with approximate standard errors in Table 27. The genetic correlations between heifer and first parity reproductive measures generally were small with no consistent sign. In addition, the approximate standard errors were large and so most estimates were not significantly different from zero. One correlation worth mentioning is the genetic correlation between AGESB and FB, which in the current study was  $-.726 \pm .09$  as compared to  $-.05 \pm .24$  reported by Hansen (27). Hansen (27) reports that the AGESB and FB are genetically unrelated where the current study reports that heifers that are older at successful breeding have fewer days from parturition to first breeding. Possible the heifers that breed at an older age are stressed less in first lactation, and therefore, come into estrus earlier. Phenotypic correlations are reported in Table 28. They tend to be slightly larger in magnitude than those reported by other researchers, but all are less than .2 and generally are less than .1 with no consistent trend in sign.

Table 26. Genetic correlations for heifer reproduction and first parity reproduction.

Heifer fertility	First parity fertility												
	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>b</sup>
AGEFB	.088	.029	-.064	-.156	-.161	-.056	-.084	-.113	-.092	-.144	-.119	-.162	-
AGESB	.213	.237	-.282	-.125	-.394	-.359	-.198	-.124	-.498	-.366	-.726	-.346	-
CRA	.121	.049	-.135	-.189	.043	.163	-.147	-.123	-.115	-.068	.148	-.131	-
CRF	.144	.083	-.142	-.218	.013	.133	-.190	-.152	-.133	-.094	.152	-.148	-
NS3	-.037	.050	.054	.138	-.193	-.291	.039	.010	-.060	-.057	-.241	-.002	-
NS9	.029	.162	-.041	.149	-.334	-.454	-.049	.001	-.123	-.008	-.291	-.029	-
EL11	.204	.263	-.251	-.122	.173	.201	-.188	-.169	-.003	-.114	.136	-.093	-
ELNS	.088	.163	-.216	-.083	.249	.217	-.054	-.070	.107	-.021	.140	-.018	-
SP91	.144	.271	-.111	.049	-.206	-.269	-.181	-.136	-.256	-.227	-.319	-.167	-
SP244	.143	.270	-.116	.049	-.206	-.269	-.179	-.136	-.255	-.227	-.320	-.167	-
DBS	.248	.210	-.250	-.212	-.132	-.101	-.275	-.271	-.272	-.307	-.169	-.276	-

<sup>a</sup>Approximate standard errors of genetic correlations are in Table 27.

<sup>b</sup>Negative estimate of genetic variance.

Table 27. Approximate standard errors of genetic correlation for heifer reproduction and first parity reproduction.

Heifer fertility	First parity fertility												
	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0305	FB	CI	DBS <sup>a</sup>
AGEFB	.127	.136	.130	.108	.149	.174	.126	.117	.134	.114	.137	.113	-
AGESB	.174	.185	.179	.146	.203	.232	.169	.156	.154	.141	.091	.142	-
CRA	.131	.140	.131	.115	.155	.177	.129	.122	.141	.122	.142	.122	-
CRF	.140	.150	.140	.123	.166	.188	.137	.131	.151	.131	.152	.131	-
NS3	.138	.147	.138	.120	.161	.184	.136	.129	.147	.127	.143	.128	-
NS9	.141	.151	.142	.122	.165	.191	.140	.131	.149	.129	.141	.129	-
EL11	.207	.219	.209	.184	.237	.269	.204	.194	.219	.190	.227	.189	-
ELNS	.226	.239	.232	.202	.260	.295	.223	.211	.240	.208	.249	.206	-
SP91	.136	.144	.135	.118	.153	.170	.134	.126	.138	.120	.129	.123	-
SP244	.136	.144	.135	.118	.153	.170	.134	.126	.138	.120	.129	.123	-
DBS	.149	.151	.148	.139	.157	.165	.149	.143	.152	.139	.165	.144	-

<sup>a</sup>Negative estimate of genetic variance

Table 28. Phenotypic correlations for heifer reproduction and first parity reproduction.

Heifer fertility	First parity fertility												
	CRA	CRF	NS3	NS9	EL11	ELNS	SP91	SP244	D0150	D0505	FB	CI	DBS
AGEFB	.053	.038	-.060	-.078	-.036	-.047	-.022	-.027	.038	.033	.126	.026	.056
AGESB	-.029	-.032	.031	.000	.011	-.024	.061	.046	.098	.094	.108	.086	.075
CRA	.167	.150	-.178	-.149	-.105	-.083	-.168	-.155	-.138	-.137	.021	-.144	-.057
CRF	.149	.131	-.159	-.146	-.085	-.060	-.152	-.146	-.119	-.126	.028	-.133	-.044
NS3	-.156	-.136	.165	.135	.092	.067	.156	.138	.133	.121	-.023	.122	.046
NS9	-.165	-.145	.177	.142	.092	.077	.156	.133	.132	.115	-.025	.119	.031
EL11	-.028	-.018	.034	.036	.058	.048	.029	.032	.043	.041	.023	.045	.001
ELNS	-.032	-.022	.035	.043	.062	.058	.029	.033	.032	.037	.013	.044	-.003
SP91	-.135	-.121	.147	.124	.078	.055	.133	.118	.115	.104	-.016	.106	.031
SP244	-.135	-.121	.147	.124	.078	.055	.133	.118	.115	.104	-.016	.106	.031
DBS	.019	.018	-.017	-.016	-.016	-.035	-.014	-.008	.004	.008	.034	.002	.018



Heifer reproduction appeared to be either unrelated or slightly negatively related to first parity reproduction as was earlier implied by the repeatability estimates (Table 19). These results are in agreement with the conclusions reported by Hansen (27), Maijala (45) and Metz and Politiek (55) but are not in agreement with the conclusions of Janson (34).

## Chapter V

### SUMMARY AND CONCLUSIONS

Heritability estimates were less than .07 for all reproductive measures in the heifer service period except age at first breeding (.2 by maximum likelihood and .13 by MIVQUEO). Similarly with exception of conception rate, none of the measures of reproductive performance had heritabilities greater than .05 for all three remaining service period groups. Conception rate measured as a trait of the male (service sire) ranged from .08 to .135 for second and third service period. Conception rate measured as female trait (sire) had heritabilities ranging from .09 to .249 for second and third service period.

Low heritability estimates obtained in this and other studies suggest that large progeny or service sire groups will be necessary to identify the small genetic differences between bulls.

Three measures of reproductive performance, DBS, EL11, and ELNS evaluated ability of cows to cycle regularly and an estimate of early embryonic death. DBS gave no indications of being heritable and EL11 and ELNS had low heritability estimates except for third and later parity, both from maximum likelihood estimates and MIVQUEO.

Where two bounds were placed on the same measure of reproductive performance, now strong conclusion could be drawn but generally the heritability estimate of the lower bound was larger or at least close to the heritability estimate of the upper bound. Apparently, beyond a certain point, increased days open, service period, and numbers of services had large environmental variances. This could have reflected preferential treatment of favored cows.

Many genetic and phenotypic correlations were forced positive due to a part-whole relationship or due to the fact they were simply different bounds for the same measure. A few correlations were in the range from .50 to .90, but many were not significantly different from zero due to large approximate standard errors.

Repeatabilities based upon pairwise comparisons were in the range from 0 to .13. The correlation of reproductive performance between heifer and first parity ranged from .01 to .06 and were generally smaller than for later parities. Repeatabilities based upon repeated measures on the same cow ranged from 0 to .12.

Predicted Differences for female (sire) and male (service sire) reproductive measures were calculated by Best Linear Unbiased Prediction. This analysis included 207 bulls which were in the data both as sire and service

sire. Correlations between proofs for male and female reproductive measures ranged from  $-.13$  to  $.13$ . These results suggest limited genetic relationship between male and female reproduction.

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APPENDIX

Appendix Table 1. Heritability estimates from general linear method (GLM) and approximate standard errors of heritabilities for heifer reproduction.

Measure	Heritability	SE
CRF (female)	.053	.033
CRF (male)	.061	.032
CRA (female)	.105	.037
CRA (male)	.076	.035
DBS (female)	0 <sup>a</sup>	.031
DBS (male)	.043	.031
AGEFB	.315	.043
AGESB	.293	.044
NS3	.207	.043
NS9	.173	.041
EL11	0 <sup>a</sup>	.041
ELNS	0 <sup>a</sup>	.041
SP91	.225	.044
SP244	.202	.044

<sup>a</sup>Negative estimate of sire variance.

Appendix Table 2. Heritability estimates from general linear method (GLM) and approximate standard errors of heritabilities for first parity reproduction.

Measure	Heritability	SE
CRF (female)	.109	.034
CRF (male)	.156	.036
CRA (female)	.212	.041
CRA (male)	.203	.041
DBS (female)	.101	.034
DBS (male)	.011	.034
D0150	.046	.042
D0305	.027	.042
NS3	.043	.032
NS9	0 <sup>a</sup>	.032
EL11	0 <sup>a</sup>	.032
ELNS	0 <sup>a</sup>	.032
SP91	.009	.030
SP244	.008	.031
FB	.060	.030
CI	0 <sup>a</sup>	.000

<sup>a</sup>Negative estimate of sire variance.

Appendix Table 3. Heritability estimates from general linear method (GLM) and approximate standard errors of heritabilities for second parity reproduction.

Measure	Heritability	SE
CRF (female)	.144	.047
CRF (male)	.126	.045
CRA (female)	.276	.055
CRA (male)	.177	.051
DBS (female)	.006	.037
DBS (male)	.048	.037
DO150	.059	.045
DO305	.043	.047
NS3	.021	.044
NS9	0 <sup>a</sup>	.044
EL11	.023	.044
ELNS	.029	.044
SP91	0 <sup>a</sup>	.044
SP244	0 <sup>a</sup>	.044
FB	0 <sup>a</sup>	.000
CI	0 <sup>a</sup>	.000

<sup>a</sup>Negative estimate of sire variance.



Appendix Table 4. Heritability estimates from general linear method (GLM) and approximate standard errors of heritabilities for third and later parities<sup>a</sup> reproduction.

Measure	Heritability	SE
CRF (female)	.161	.037
CRF (male)	.111	.034
CRA (female)	.287	.046
CRA (male)	.110	.042
DBS (female)	0 <sup>b</sup>	.032
DBS (male)	.028	.032
D0150	.060	.062
D0305	0 <sup>b</sup>	.064
NS3	.144	.039
NS9	.212	.044
EL11	.101	.036
ELNS	.088	.035
SP91	.138	.039
SP244	.111	.041
FB	0 <sup>b</sup>	.000
CI	0 <sup>b</sup>	.000

<sup>a</sup>Third and later parities were pooled for all analysis.

<sup>b</sup>Negative estimate of sire variances.

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