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DISSERTATION

GENOTYPE BY ENVIRONMENT INTERACTION FOR HOLSTEIN MILK YIELD AND FITNESS TRAITS BETWEEN SAUDI ARABIA AND THE UNITED STATES

Submitted by

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Department of Animal Sciences

In Partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

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March 27, 2002

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY FAHAD SOLIMAN AL-HUR ENTITLED GENOTYPE BY ENVIRONMENT INTERACTION FOR HOLSTEIN MILK YIELD AND FITNESS TRAITS BETWEEN SAUDI ARABIA AND THE UNITED STATES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

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ABSTRACT OF DISSERTATION

GENOTYPE BY ENVIRONMENT INTERACTION FOR HOLSTEIN MILK YIELD AND FITNESS TRAITS BETWEEN SAUDI ARABIA AND THE UNITED STATES

(Co)variance components and genetic parameters for Holstein first and all lactations mature equivalent milk and reproductive traits in the first four lactations were estimated by multiple-trait animal model using Method R procedures. The objectives of this study were to determine if genotype by environment interactions for milk yield and fitness traits exist between Saudi Arabia and the US and to investigate the relationship between milk yield and reproductive performance under a Saudi environment.

The Saudi data included 46,777 records from 20,815 cows, daughters of 255 bulls and the US data included 38,293 records from 19,456 cows, daughters of 176 bulls. There were 151 sires common to both countries with average number of daughters 260 in the Saudi data and 246 in the US data. Herd-year-season was identified separately for first and multiple calving cows. Estimates of genetic correlations for milk yield between the two regions in first and all lactations were .68 and .17, respectively. In first lactation analysis, additive genetic variances were similar but residual variance was 21% smaller in Saudi Arabia than in the US. In the all-lactations analysis, additive genetic variance was 20% smaller for Saudi Arabia than for the US but residual variances were similar. Genetic correlations for gestation length and calving interval between the two countries were .96 and .99, respectively and the genetic correlation for age at first calving was low (0.10). The heritability estimate of the first lactation milk yield in Saudi Arabia (.29) was

larger than the estimate in the US (.24) but the estimate from all lactations in the US (.34) was larger than the estimate in Saudi Arabia (.29). Phenotypic and environmental correlations between yield and fertility traits were positive (unfavorable). Genetic correlations between yield and days open, calving interval, number of services per conception, gestation length, and age at first calving were .44, .51, .19, -.05, and -.08, respectively. These results substantiate the presence of genotype by environment interaction for milk yield and age at first calving. Therefore, selection from within the Saudi Holstein population may be the best tool to identify the optimal animal for Saudi dairy production.

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DEDICATION

To my mother, without whose prayers and patience I might not have been able to achieve this goal. Thank you for your continual prayers during prayer time and through the phone. To my father Soliman who have bestowed upon me the importance of education but passed on before he saw this achievement. I pray to Allah to bestow on him his forgiveness, his mercy, and make paradise his eternal home. To my wife and children, thank you for everything you did for me, none of this would be possible without your love and patience.

TABLE OF CONTENTC

LIST OF TABLES

Chapter 1

INTRODUCTION

Saudi Arabia is one of the driest countries in the world, with an average rainfall of less than 5 inches per year. Marked seasons in the temperate sense do not exist. Summer is hot with temperatures in most areas approaching 49° C (120° F). Winter is cooler with an average temperature of 14° C (58° F) in the central region. Traditional livestock production in this country uses local breeds, which are characterized by low milk yield, slow growth rate, and high mortality rate. Because of high population growth rate and improvement in the standard of living, demand for milk and dairy production increased. Therefore, in the late 1970's and early 1980's and with the help of booming oil prices, the government of Saudi Arabia decided to attain self-sufficiency in food production. A massive agricultural development program was started to enhance food production in the kingdom. A five-year target period was set for achieving self-sufficiency in dairy products by motivating private investors through substantial government subsidies and financial incentives to establish modern, successful dairy farms. The fastest way to achieve this goal was through the importation of semen and live animals from highly selected breeds of dairy cattle such as Holstein and Jersey from developed countries, mainly the United States of America. About 39 specialized dairy projects were established by 1996, comprising 58,943 cows and producing 453,000 tons of milk a year. A higher percentage of these enterprises are located in the central region.

In Saudi Arabia, where suitable native cattle for commercial dairying are not available, introduction of highly selected breeds has been very important. However, The importation of germplasm from a temperate country, namely the United States, to a country with these climatic characteristics raises an important question about the performance of animals not bred for a harsh environment. Relationships between performances of these breeds in both environments must be studied to determine the impact of the different environments on production and reproductive traits. It is widely established that if a genotype is developed under particular environmental conditions but reared under different environmental conditions, then investigation of genotype-environment interaction becomes important. The question is whether superior genotypes in a favorable environment are also superior in a less favorable environment. In other words, how much of the genetic superiority of the best bulls in the better environment will be manifested in the poorer environment. If the investigation reveals a violation of any of the two following assumptions, then there is interaction. The first assumption is that different environment conditions have the same effect on different genotypes, and the second is that phenotypic and genetic variances are homogeneous across environments (Cromie et al., 1998; Stanton, 1990).

The classic example of genotype by environment (G x E) interaction occurs when the first assumption is violated. In this case, the genetic correlation between a trait expressed in one environment and the same trait expressed in another environment is no longer unity. This indicates that different sets of genes control the trait in different environments. Consequently, individual breeding values may change rank from one environment to the other.

If the second assumption is violated then another form of G x E interaction occurs. Breeding values for single trait do not change rank across environments, instead the magnitude of differences between animals is not the same across environments. This form of interaction results from heterogeneous variances. Even if genetic correlations between traits expressed in different countries are equal to unity, genetic and phenotypic variances are likely to vary from temperate to arid countries.

An important concern when importing germplasm from temperate to arid environments is that daughters of highly selected sires for milk yield may have lower fitness as a result of the stress of production and harsh environment. It is conceivable that when transferring cows from more favorable to less favorable environments, genes controlling fitness traits may differ (Abubaker, 1985). In fact the effect of G x E interaction may be more pronounced with lowly heritable traits such as fertility traits than other traits (Bourdon, 1997). Therefore, the question becomes: should Saudi dairymen use semen from high, average or low yield sires from temperate countries as a way to obtain optimum production and reproduction.

Economic returns of dairy projects depend heavily upon average herdlife of the cows. The two major factors that affect this average are milk yield and reproductive efficiency. The more frequent births a cow gives, the greater amount of milk produced. More important is to know the relationship between the two factors and how they interact in different lactations. Combining records of production and reproduction from more than one lactation results in better understanding of the nature of the relationship between milk yield and fertility traits because the relationship within a given lactation can be different from that across lactations (Hayes et al., 1992; and Schaeffer and Henderson,

1972).

The objectives of this study were:

(1) To determine whether interactions between genotype and environment for milk and fitness traits in daughters of sires used in the United States and Saudi Arabia exist by estimating and comparing genetic, residual, and phenotypic variances and genetic co(variances) across environments from a multi-trait animal model.

(2) To evaluate the performance of Holsteins in Saudi Arabia by deriving estimates of genetic parameters and predicting breeding values of animals.

(3) To estimate genetic, environment and phenotypic correlations between milk production in the first three lactations and between production and fitness traits across lactations and within each of the first three lactations.

CHAPTER 2

LITERATURE REVIEW

Genotype by Environment Interaction

Definition and General Review

With the wide use of artificial insemination, considerable attention has been focused on genotype by environment interaction for dairy production traits (Peterson, 1975, Stanton et al., 1991). Genotype by environment interactions could arise if a genotype is tested in one environment, but used in a different environment, because different genotypes differ in their phenotypic expression across environments (Lytton and Legates, 1966; Taneja and Rao, 1982; Togashi et al., 1999). Numerous researchers have investigated genotype by environment interactions in dairy cattle. It was first suggested by Wright in 1939 that if interaction between genotype and environment exist, a specific race should be bred for each environment. Lush (1945) recommended that breeding stock selection should be conducted in similar environmental conditions to those in which the animals would perform. Pioneer studies to investigate the importance of the interaction between genotype and environment in relation to animal breeding were carried out by Hammond (1947), Falconer (1952), Falconer and Latyszewsky (1952), and Yamada (1962).

The definitions of the different environments in this sense could be different climates (Branton et al., 1974), regions (Lytton and Legates, 1966; Dickinson et al.,

1976; and Carabano et al., 1990), states (Wade and Van Vleck, 1989), parities (Banos and Shook, 1990; Ron et al., 1983), levels of nutrition or management (Veerkamp et al., 1994; Wang et al., 1992) or countries (Abubakar et al., 1987a; Carabano et al., 1989; Cienfuegos-Rivas et al., 1998; Charagu and Peterson, 1998; Metzger et al., 1994; Petersen, 1975; Powell and Dickinson, 1977; Stanton et al., 1991).

Branton et al. (1974) investigated the interaction of genotype by climate in Louisiana Holstein herds and concluded that this interaction is not important for milk and fat yield. Lytton and Legates (1966), in a study of Holstein sires with daughters in the northern and southern regions of the United States, found the rank of sires in both regions virtually unchanged. Similar results were reported by Carabano et al. (1990) for three regions of the United States. The same trend was observed when records from different states were studied (Wade and Van Vleck, 1989). It could, therefore, be concluded that climatic differences between herds, regions, and state within a country are not important sources of classic interaction.

However, when countries were defined as different environments, mixed results were reported. In a well planned identical twin heifer calves experiment where eight sets of temperate breed twins were divided between New Zealand and Fiji, Payne and Hancock (1967) observed significant reduction in milk yield in the first lactation from six twins in Fiji. Although management levels and feeding were identical, the six co-twins in New Zealand produced 44% more milk than their pair twins in Fiji. However, Fiji climate stress did not affect the twins uniformly, as some twins produced as much milk as their co-twins in New Zealand. This suggests that individual temperate heifers from the same breed reacted differently to environmental stress. Cunningham and O'Byrne (1977)

compared progeny tests of bulls used in Ireland with tests of their sires used in Britain. They estimated a genetic correlation between milk yield in the two environments to be only 0.6, implying a large genotype by environment interaction between Ireland and Britain. Significant genotype by environment interaction was also reported by Romero (1986) between Puerto Rico and North America and by Abubakar (1987) between Mexico and Colombia and North America. Carabano (1989) reported similar result for fat but not milk between United States and Spain. Cienfuegos-Rivas et al. (1998) studied the interaction of first lactation milk yield between Holstein cows in the United States and Mexico and reported a genetic correlation that significantly deviated from unity.

However, this view was not upheld by other researchers since little evidence of an interaction was deduced. In a study of Holstein records from the United States and Latin America as represented by Colombia, Mexico, and Puerto Rico, Stanton et al (1991) found that sires from the United States ranked the same in Latin America. This indicates a lack of genotype by environment interaction in the classic sense (i.e., the genetic correlation between the same trait expressed in different environments substantially deviating from unity), although large differences in variation were observed (Stanton et al., 1991). Carabano et al. (1989) reported an average genetic correlation between milk yield expressed under Spanish conditions and milk yield expressed under United States conditions of 0.81 from Holsteins. The same conclusion was reported by Metzger et al. (1994) for Jersey milk production in the United States and Denmark. Petersen (1975) reported high correlations between sire breeding values in two European countries (Denmark and Bulgaria).

Forms of Genotype by Environment Interaction

Differences in the expression of genotypes between environments can be attributed to two different types of genotype by environment interaction. The first type is the change of rank of breeding values of bulls for a particular trait from one environment to the other (Togashi et al., 1999). In other words, there is a substantial deviation from unity of the correlation between the breeding values obtained for animals in different environments indicating that different genes may control the trait in different environments. This type is the usual or classic form of genotype by environment interaction (Van Vleck, 1963; and Stanton, 1991). Falconer (1952) pointed out that this type of interaction could be measured by the genetic correlation between the performances of the same genotype expressed in two environments. In this case records of the same trait in different environments are considered as two different but genetically correlated traits. The magnitude of the estimated genetic correlation reflects the extent to which the same genes control both traits. Few workers reported significant interaction of this form for milk yield. Buvanendran and Peterson (1980) reported a very low genetic correlation 0.08 between milk yield in Denmark and Sri Lanka. Cunnigham an O'Byrne (1977) reported a moderate genetic correlation of 0.60 for milk yields in Britain and Ireland. Abubakar et al. (1985) found that the correlation between the ranks of the breeding values of 17 sires with daughters in Colombia and Mexico was 0.26. The authors attributed the low correlation estimate to more stressful environment conditions in Colombia compared to Mexico. In their study, Cienfuegos-Rivas et al. (1998) tried to investigate wither data from low production herds in United States are better predictors of performance in Mexico. These authors divided 55,162 first lactation records from

Mexico based on herd-year standard deviation into low (<1,300 kg) and high (>1,600 kg) and identified the low (<1025 kg) subset from 499,401 first lactation records from United States. There were 474 sires common to both countries. Genetic correlations between all data from the United States with all, high, and low subsets from Mexico were 0.63, 0.71, and 0.60, respectively. Correlations between the low subset from United States and low and high subsets from Mexico were 0.72 and 0.93. This result implies that considerable reranking of sires occurs and that performance of daughters of a given sire in Mexico is better predicted from the performance of daughters of that sire in a low environment in the United States.

However, other workers investigated genotype by environment interaction for milk yield for different breeds, for example, Red Danish in Denmark and Bulgaria and Czechoslovakia (Petersen, 1975), Holstein milk yield in the United States and Spain (Carabano et al., 1989), and in the United States and Latin America (Stanton et al., 1991), and Jersey milk yield in United States and Spain (Metzger et al., 1994) but reported large estimates of genetic correlation, indicating that genotypes will rank similarly in the countries studied.

Stanton et al. (1991) studied the cause for heterogeneous response in milk yield for daughters of sires from the United States and Latin America. The authors divided the data from Latin America by countries (Colombia, Mexico, and Puerto Rico) and by herd-year standard deviation (HYSD) to high HYSD (≥ 1300 kg) and low HYSD (< 1200 kg). Two variables for milk yield, mature equivalent milk (ME milk) production and weighted milk calculated as ((ME = milk/HYSD) x 1000) were studied. Genetic correlation estimates from five joint analyses pairing the United States with Latin America, Mexico,

Colombia, high HYSD, and low HYSD, were 0.91, 0.90, 0.78, 0.89, 0.78, respectively. Coefficient for the expected correlated response for mature equivalent milk yield in Latin America, high HYSD, low HYSD, Mexico, and Colombia when selection is in sire performance in the United States were .70, .79, .53, .78, .56, respectively. Although genetic correlations were high between yields in North America and Latin America, response was not pronounced, particularly in low HYSD herds and in Colombia, because if the difference between estimated transmitting abilities for two sires in the United States is 100 kg, average differences between the daughters of the same two sires under Low HYSD or Colombia will be approximately 50 kg. The authors suggested that reduced sire and residual variances caused performance to differ between regions. This type of interaction will be discussed next.

The second type of genetic by environment interaction occurs when genetic and residual variation is substantially different across environments. Hammond (1947) pointed out that it is the environment to which the animal is exposed that allows genetic variance to be expressed. In any given environment, animals with high potential genetic merit would always outrank those animals with lowest merit, but differences between animals would vary according to environmental opportunity (Hammond, 1947). Dickerson (1962) called this type of interaction a pseudo interaction. Dickerson (1962) suggested that although genetic correlations may be one, adjustment should be made for differences in genetic variation across environments because residual variance could cause a pseudo interaction. This type of interaction is also described as 'environmental sensitivity' by Falconer (1993).

Heterogeneity of genetic and environmental variances for milk yield is widely observed (Danell, 1982; Lofgren et al, 1985; De Veer and Van Vleck, 1987; Winkelman,

1988; Famula, 1989; Dong and Mao, 1990; and Weigel et al, 1993). Genetic variation can be truncated by different gene response in different environments if 1) some genes effects are nil in poor environments or 2) if average gene effects are suppressed by the less favorable environment (Short et al., 1990).

Some reports showed that genetic and residual variances increased as herd average milk production increased (Van Vleck, 1963; DeVeer and Van Vleck , 1987; Boldman and Freeman, 1990; Dong and Maw, 1990; and Weigel et all, 1993). Van Vleck (1963) studied first and second lactation records of New York Holsteins. He divided the data into four groups according to herd-mate averages. He found that both genetic and nongenetic variation increased in the more favorable environment. However, Famula (1989) concluded that classifying herds by mean yield could bias genetic and residual variances. Transformation has been used to adjust for the relation between mean and variance (DeVeer and Van Vleck, 1987; and Hill et al., 1983; and Wade and Van Vleck, 1989). DeVeer and Van Vleck (1987) divided the data based on mean milk yield to four groups but also to untransformed and logarithm transformed records. They reported that for untransformed records sire and residual variances increased as production increased. However when records were transformed the sire component remained constant and residual variance decreased as production increased. Similar trends were observed by other researchers who used different approaches from the traditional classification of records on mean yield. Records were split by within-herd variation (Lofgren et al., 1985; and Stanton et al., 1991) or by variance and coefficient of variation (Brotherstone and Hill, 1986; and Hill et al., 1983). In their study Stanton et al. (1991) used a sire model to analyze first lactation mature equivalent milk records from

the United States and Latin America (Colombia, Mexico, and Puerto Rico). Though genetic correlation were high (0.91), substantial differences in variance for milk between the US and Latin America were observed. Sire and residual variances were 41 and 29% smaller in Latin America than in the United States. It could, therefore, be concluded from the reports discussed that this form of genotype by environment is observed and reported more often than the classic form. In fact most of the studies that documented the classic form of genotype by environment interaction also reported the second type of interaction. Therefore, it would be beneficial to review the effect of heterogeneous variation on genetic parameter estimates.

Heterogeneous Variation and Estimation of Heritability

As discussed in the forgoing pages the magnitude of genetic and residual variation may vary across herds and environments. More important, however, is the change of the fraction of additive variance because that would result in different genetic parameter estimates for milk yield under different levels of production, herd variances, regions, states, or countries, eventually affecting was the choice of animals to be selected. Robertson et al. (1960) concluded that the type of interaction that is caused by heterogeneous variance reflects the impact of the environment on the accuracy of selecting superior animals. Different heritability estimates, for example, would result in different predictions and may increase or decrease the time for a given animal to reach to a certain level of accuracy. If the trait is lowly heritable, more daughters must be tested to obtain a fixed accuracy than if the trait is highly heritable (Bourdon, 1997; Van Tassell et al., 1999). Young sires are primarily affected by increased heritability because they

attain extreme PTA and reliability with smaller numbers of descendants. Therefore, faster genetic improvement can be achieved by identifying those sires earlier (Van Tassell et al., 1999).

Four situations can arise with heterogeneous variation across environments:

The first is when genetic variances are equal but residual variances are different. In this case, the fraction of total variance that can be attributed to genetic variance (heritability) changes.

The second situation is when additive genetic variances are not the same across environments, but residual variances are equal. Heritability also changes.

In the third situation both additive and residual variances in both environments change proportion lately. In this case heritability will be constant.

In the last situation both additive and residual variances across environments change independently from each other resulting in different heritabilities.

Numerous studies suggest an increase in heritability estimates associated with improvement in environment. Van Tassell et al. (1999) used Method R to obtain genetic parameters for first lactation data. The authors divided the data based on within-herd-year standard deviation and found that heritability estimates increased with increased HYSD. Hill et al. (1983) studied first lactation milk yield records from Friesian-Holsteins in England and Wales. The authors divided the records by herd level, transformed to log and untransformed, variance, and coefficient of variation. Estimates of heritability were 0.25 at the low level and 0.30 at the high level when data were split based on mean level of production and 0.25 and 0.35 when data were split on log

transformed data. When data were split on variance the corresponding estimates were 0.24 and 0.36, and when split on coefficient of variation, 0.22 and 0.32. De Veer and Van Vleck (1987) reported that heritability estimates from linear and transformed records increased as production increased.

Banos and Shook (1990) found tendencies for decreased genetic variance, increased residual variance and decreased heritability for milk yield as parity increased. Heritability estimates ranged from 0.26 in the first parity to 0.17 in the third parity from models with and without sire by herd interaction effects. However, Dematawewa and Berger (1998) observed otherwise for heritability of milk records adjusted only for 305 days and not parity. The authors reported that phenotypic variance was reduced more relative to additive variance resulted in increasing heritability estimates in later parities.

These results were in contrast with results by Burnside and Rennie (1961), and Robertson et al. (1960) who reported heterogeneous genetic and phenotypic variation associated with different levels of milk production. Heritability remained relatively unchanged over different herd means. Van Vleck and Bradford (1964) used dam-daughter regression and paternal half-sib correlation to obtain estimates of heritability. They reported that heritability estimates increased as yield increased only when the paternal half-sib correlation was used. But at ten levels of environments, heritability estimates by dam-daughter regression were constant. Similar results were reported by Wade and Van Vleck (1989) using the same methodology (dam-daughter regression). Lafgren et al. (1985) pointed out that heritability for Holstein milk yield was lowest at average levels and greatest at the extremes. However, when herds were split on herd standard deviation, heritability increased slightly as herd standard deviation increased.

Fertility and milk Production

Relationship Between Fertility Traits and Milk Yield

The primary selection target in dairy breeding has been increasing milk yield (Dematawewa and Berger, 1998). However, other traits such as fertility are also important to increase profitability of dairy projects (Holmann et al., 1984; Strandberg and Oltenacu, 1989). Profitability and longevity of dairy cows are directly affected by reproductive efficiency, because the amount of milk produced per cow per day of herd life is influenced by fertility (Hageman et al., 1991). Most researchers (Abdallah and McDaniel et al., 2000; Berger et al., 1981; Dematawewa and Berger, 1998; Everett et al., 1966; Hansen et al., 1983; Pryce et al., 2000; Seykora and McDaniel, 1982; Weller, 1989) who studied the relationship between milk production and reproductive traits in dairy cows found marked genetic antagonism between yield of milk and female fertility. That is, reproductive performance may deteriorate as a result of increasing milk production (Faust et al., 1989; Kragelund et al., 1979). Other researchers reported a modest effect (Hageman et al., 1991), and others (Adkinson et al., 1977; Dong and Van Vleck, 1989; Shanks et al., 1978) concluded that little association between milk yield and cow fertility exists. In a designed, single-trait selection experiment, Shanks et al. (1978) found no major association between yield and fertility. Laben et al. (1981) pointed out a depression in fertility associated with increasing yield but concluded that this depression is not so great as to prevent good reproductive performance among high yielding cows.

Other traits such as culling rate and herd life are sensitive to fertility performance. A substantial proportion of all cow disposals is attributed to reproductive failure- about 16% of Holsteins in United States (Freeman, 1984; Miller et al., 1966; White and

Nichols, 1965), 25% in Canada (Westell et all., 1982), 28% in western Europe (Philipsson, 1981), and 27% in Israel (Heiman, 1979). Reproductive disorders accounted for 21% of the total health cost of herds in United States (Shanks and Freeman, 1979). Berger et al. (1981) reviewed some studies and found that reproductive disorders and insemination costs account for 40% of the direct health costs to dairymen and that culling attributed to low fertility ranked second to low milk production as a major reason for culling. These costs are the same for high and low genetic lines for milk production (Shanks et al., 1978; Short et al., 1990a). Campos et al. (1995) estimated net returns before and after adjusting for reproductive losses for Holsteins and Jerseys and reported a substantial reduction in net returns after adjustment. The reduction amounted to 47 to 53% of predicted net returns for Holsteins and 27 to 31% for Jerseys. The authors concluded that not adjusting for reproductive losses would result in overestimation of net returns. Thus it is very important to understand the nature of the relationship between production and reproduction in order to enhance the ability of the breeder to achieve improvement in the primary trait without causing deterioration in secondary traits.

Genetic and Phenotypic Correlations Between Production and Fertility

Reproductive performance in cattle is usually represented by traits such as number of services per conception, age at first calving, calving interval, days open, and gestation length. Campos et al. (1993) concluded that increasing stress from producing milk may be the way that genetic merit for milk affects reproduction, especially in warm or hot climates. According to the International Bull Evaluation Service (INTERBULL, 1992) genetic evaluation procedures used in 12 of 28 countries use adjustment factors for

the relation between reproduction and yield. Most of the studies (Abdallah and Berger, 2000; Dematawewa and Berger, 1998; Campos et al., 1994; Hansen et al., 1983; Hermas et al., 1987; More et al., 1992; Pryce et al., 2000; VanRaden et al., 1987; Weller, 1989) that estimated genetic correlations between milk yield and female fertility reported unfavorable correlations. Many factors have been implicated to cause an association between yield and reproduction: nutrition, management (Hayes et al., 1992), season and environment, age of cow (Berger et al., 1981), and genetic factors (Dematawewa and Berger, 1998). Of these, genetic factors are the most important to animal breeding. In the following sections, genetic and phenotypic relationships between milk yield and several reproductive traits are reviewed. Throughout this review, high and low herd production would reflect favorable and unfavorable environments.

Days open and milk yield

Days open is the period from parturition until successful insemination. It is composed of two distinct periods. The first is from parturition to first breeding. This period is constant based on the management practice. The second period is variable and is from first breeding to conception. Therefore, variance in days open is determined entirely by the second period within a given management system. Four to 8% of the variation in milk is attributed to variation in days open (Smith and Legates, 1962; Ripley et al., 1970). Olds et al. (1979) found that 7% of the variation in days open is attributed to 120-day milk and that 4.5 kg more of 305-day milk resulted from each additional day open. Slama et al. (1976) concluded that differences in detection of estrus is the major cause of the antagonism of milk on fertility performance, implying that this problem can

be overcome by good management practice. Laben et al. (1982) found that the highest yielding herds with better management, specifically in detection of estrus, averaged 21 days fewer days open than herds with lower milk yield. Wiggans and Ernst (1987) found that cows in herds with high milk production had, on average, 16 fewer days open than cows in low yielding herds. This result was later supported by reports by Nebel and Mcgiliard (1993) who observed a trend of decreasing days open as yield increased.

In contrast several studies reported an increment in milk production associated with longer days open or vice versa (Kelm et al., 1997; Lee et al., 1997; Marti and Funk, 1994; Sadek et al., 1988). Findings by Lee et al. (1997) suggested a greater impact of current days open in early lactation rather than later and on second parity rather than first. As current days open in first parity increased from 30 to 100 days, yield increased by 876 kg, but increment in yield was 172 kg when days open increased from 100 to 200 days (Lee et al., 1997). Dematawewa and Berger (1998) investigated the relationship between milk yield and several reproductive traits in the first three parities of Holstein cows and found a strong positive (antagonistic) correlation between fertility and yield. The authors reported genetic and phenotypic correlations between yield and days open of 0.55 and 0.27, 0.63 and 0.3, and 0.64 and 0.31 for first, second, and third lactation, respectively. Berger et al. (1981) reported substantial higher genetic correlations between yield and days open in first lactation (0.62 ± 0.14) than in second (0.15 ± 0.15) and third (0.18 ± 0.9). They concluded that since selection is practiced after the first lactation, correlations involving first lactation are the most reliable. Similarly high genetic correlations at first parity (0.35 to .60) were reported by Seykora and McDaniel (1983) who analyzed lactation records from 1950 to 1980 using paternal half-sister analysis and cow-dam

regression. Fonseca et al. (1983) reported a positive linear relation between days open and milk yield in Jerseys cows. These findings indicate that higher producing cows were bred later than lower producers. After reporting a moderate genetic correlation of 0.43 between fat corrected milk and days open, Mantysaar and Van Vleck (1989) recommended a multi-trait index including milk yield and days open because selection only for yield would result in deterioration in reproductive efficiency. This view was not upheld by Smith and Legates (1962), who concluded that even if the genetic correlation is 1.00 between yield and days open, little consequence on reproductive traits is expected because the genetic variance of days open composes a small part of phenotypic variance. Everett et al. (1966) reported a phenotypic correlation between days open and 120-day milk production that was essentially zero. This is supported by findings by Raheja et al. (1989a) who found phenotypic correlations between days open and production traits in the first three lactations to be nil.

Calving Interval and Milk Yield

Calving interval is the number of days between two consecutive parturitions and is the sum of days open and gestation length. Because it is influenced by all reproductive traits, Dong and Van Vleck (1989) used calving interval to estimate the covariance between milk yield and reproduction. Call and Stevenson (1985) reviewed several studies and suggested that maximum annual return was associated with calving intervals of 12 and 13 months and declined with greater intervals. However, Holmann et al. (1984) concluded that calving intervals of 12 to 15 months had minimal effect on annual income, but when days open were considered, a 13-month period was optimal. It has

been suggested that 13 and 12 months are the optimal calving interval for primiparous and multiparous cows, respectively. Although disagreement exists on optimum calving interval, prolonged calving interval and reduction of milk production were the two main reasons for the economic loss resulting from low fertility (Miller et al., 1967; Olds et al., 1979). Several researchers investigated the relationship between milk production and calving interval and pointed out the existence of a positive (unfavorable) relationship (Hageman et al., 1991; Miller et al., 1967; Pedron et al., 1989; Ray et al., 1992; Short et al., 1990). This was attributed to the prevention of early return to estrus due to the strong negative energy balance in early lactation (Butler et al., 1981). Hageman et al. (1991) studied reproductive performance in first and second lactations in different genetic lines created by selection of sires differing in their estimated transmitting ability for milk production by 450 kg. For both parities, Hageman et al. (1991) found that calving interval increased significantly as milk yield increased. As milk production in the midrange yield class increased by 1000 kg, calving interval increased by 7.4 days in first and 13.7 days in second parity. Ray et al. (1992) reported partial regression coefficients of calving interval on milk of 12 days increase in calving interval associated with 1000 kg of milk production. Everett et al. (1966) reported high genetic correlations, 0.46 for Holsteins and 0.51 for Guernseys, between 120-day milk and calving interval, but concluded that because heritability of reproductive traits is near zero, consequence in breeding efficiency due to selection for milk production would be insignificant. Dong and Van Vleck (1989) used the REML expectation-maximization algorithm with an animal model to estimate covariance between milk yield and calving interval. They reported a low genetic correlation of .09, indicating that genetic ability to produce more milk would not change breeding efficiency materially.

Although it is well known that selection has in the last 50 years increased milk production substantially, a report by Silva et al. (1992), who studied reproductive traits including calving interval in Florida dairy cattle over 52-year period, revealed no phenotypic trend for calving interval. This suggests that calving interval neither deteriorates nor improves with higher milk production (Silva et al., 1992). Similar results were found earlier by Nieuwhof et al. (1989). However, El Amin et al. (1986) found that calving interval increased with time in their study, 1955 to 1977, for different crosses of European breeds and Butana cattle in tropical Sudan. Short et al. (1990b) studied calving interval of different classes based on time periods and herd-year standard deviation for milk yield in first and second parities for grade Holstein cows. They reported that although mean calving interval increased as standard deviation of yield increased in all time periods and parities, no trend of sire components of variance of calving interval associated with standard deviation of milk was noticed. Increment in residual variance was observed as standard deviation of yield increased in both parities within each time period, but not with time periods per se (Short et al. (1990b).

Age at First Calving and Milk Yield

Age at first calving is considered to be one of the most important traits that affect both production and reproduction life of the female. Increasing the productive life of females, decreasing replacement cost, and speeding genetic progress by reducing generation interval are some advantages of breeding dairy heifers at younger age (Gill and Allaire, 1976; Lin et al., 1986; Simerl et al., 1991). Some disadvantage may include increasing incidence of dystocia and calf mortality and a negative effect on first parity production (Lin et al., 1986; Pirlo et al., 2000; Simerl et al., 1991).

Several studies reported that reduction in age at first calving increased milk yield per day of life (Gardener et al., 1977; Gill and Allaire, 1976; Lin et al., 1988). A one-month decrease in age at first calving increased total milk yield of three-parities and 61 months by 427 and 554 kg of milk, respectively (Lin et al., 1988). To maximize life-time performance, Gill and Allaire (1976) suggested an age at first parturition between 22.5 to 23.5 months. Pirlo et al. (2000) suggested 23 and 24 months under Italian economic conditions. However Thompson et al. (1983) found that age at first calving and calving difficulty are not related and suggested that timing of breeding heifers should be based on size rather than age. Simerl and Wilcox (1991) found that heifers calving for the first time at ages less than 22 or more than 27 months are more likely to have calving problems.

Hermas et al. (1987) studied first lactation production and reproduction records of Guernsey cows taken from 1958 to 1981 in two experimental station herds. Although the phenotypic correlation was near zero (-.01), a high and favorable genetic correlation (-.78) between milk yield and age at first calving was obtained, implying that selection for high milk production resulted in heifers that calve at younger ages (Hermas et al., 1987). Similar results were reported by McDaniel and El-Sayel (1980). A substantially lower genetic correlation (-.06) was reported by Moore et al. (1992) for Holstein cows, but the same study revealed a moderate genetic correlation (-.45) for Ayrshire cows. The phenotypic correlations in their study were positive but low (.06) and similar in both breeds.

Gestation Length and Number of Services per Conception

Gestation length is days from successful service to subsequent parturition. Hageman et al. (1991) found significantly (P <.01) longer gestation length between

genetic lines differing in transmitting ability for milk production. However, real differences were small, cows from the high milking yield lines had a gestation length that is one day longer than cows from the low milk yield lines. Other researchers investigating the correlated response in reproduction to selection for milk from long term selection projects in Jerseys and Holsteins came to the same conclusion (Bonczek et al., 1992; Rothschild et al., 1981). Other researchers (i.e., Silva et al., 1992) observed an increase in gestation length associated with advancing lactation number.

Number of services is considered by some researchers (i.e., Nebel and McGilliard, 1993) to be more important than days open and calving interval as an indicator of female fertility efficiency. It represents the cumulative number of inseminations that the cow receives in a given parity. Faust et al. (1988) studied the relationship between female reproductive performance as represented by conception rate and number of services at three levels of milk production and found a marked positive trend in number of breedings with increased milk production. The same study showed that a 12% (approximately) decline in first service conception rate and 28% increase in number of services per 1000 kg of milk yield in the midrange and high production groups. Reproductive performance of the cows in the lowest production group was not affected. Olds et al. (1979) found greater number of services resulted from higher 120-day milk production. Marked effects start at about 1,000 kg of 120-day milk and increase thereafter, with heifers being slightly more affected than cows. Wiggans and Ernst (1987) reported an average of 2.4 services per conception, but found that cows in herds with high milk yield averaged 0.2 services more than cows in low yielding herds. Maijala (1976) pointed out an increase in number of services per conception associated with increase in herd average milk yield in Finnish cows. As age of cows increases, milk

production increases and, therefore, more services per conception are needed (Moore et al., 1992). Using an animal model, Weller and Ezra (1997) reported a negative genetic correlation (unfavorable) of –0.286 and a small but positive phenotypic correlation of 0.037 between yield in Israeli Holsteins and conception index, defined as the inverse of the number of breedings to conception. This agrees with findings by Faust et al. (1989) who reported genetic correlations between number of services and milk yield of 0.354 and 0.445 from daughter-dam regressions and paternal half-sib analyses, respectively. However, a small but favorable correlation of -0.04 was reported by Boyd et al. (1954). In their study, Raheja et al. (1989a) showed no genetic or phenotypic association between milk and number of services in the first three lactations. Across parities, Hansen et al. (1983) found smaller genetic correlations between milk and fertility in second than in first parity.

Genetic Parameters for Milk Yield

Heritability

For an animal breeding plan to be successful, knowledge of genetic and phenotypic components of variance is essential. The general conclusion that can be drawn from most of the studies that reported heritability estimates of milk production is that estimates vary according to method of estimation, herd level or standard deviation of production, size and nature of the data set, and editing of the data (Abubakar, 1985; Carabano et al., 1990; Chauhan and Hhayes, 1991; DeVeer and VanVleck, 1987; Dong et al., 1988; Fuerst and Solkner, 1994; Lofgren et al., 1986; Maijala, 1974; Ndlovu, 1993; Norman et al., 1991; Stanton et al., 1991). Estimates of heritability for milk production ranged from 0.10 to .60. Many different methods were used to obtain variance

components from which heritability was estimated. Van Vleck and Bradford (1965) found that estimates of heritability from paternal half-sib correlations for first lactation were lower than those from regression of daughter on dam. Because heifers are selected or culled based on first lactation performance, and to avoid selection bias, most estimates of heritability from procedures preceding the introduction of animal models were based on first lactation performance or assumed a genetic correlation of 1.0 between all lactations (Swalve and Van Vlek, 1987). Nowadays, using animal-model procedures instead of evaluating sires or cows separately to predict breeding values is widely accepted in dairy cattle evaluation. Because animal models use all relationships between animals, estimates of heritability may be enhanced (Dong and Van Vleck, 1989; Swalve and Van Vlek, 1987).

Estimates of heritability are also reported to differ with age. Berger et al. (1981), using a paternal half-sib correlation method, reported heritability estimates for 305-day fat corrected milk of 0.24 for first, 0.18 for second, and 0.14 for third parity. The work of Swalve and Van Vleck (1987) was the pioneer study that introduced the animal model to the estimation of genetic parameters in dairy cattle. They studied the genetic relationships between the first three lactation records and obtained higher heritability estimates than had been commonly reported. Heritability estimates in their study, however, did not decrease as parity increased and were 0.33 for first, 0.33 for second, and 0.34 for third lactation.

Repeatability

Repeatability estimates may also be affected by method of estimation and model used (Romero, 1986). Repeatability has been used to predict future production from

earlier records. If the relation between the parities in question is high, then the conclusion is that both parities may be affected by the same genes and by the same permanent environmental factors and that earlier records are good predictors of later records. Thus selection can be based in earlier records. The magnitude of this parameter for milk yield as used by the USDA Dairy Herd Improvement Association for sire evaluation is 0.55 (Van Tassell et al. 1999). Romero (1986) reviewed the literature and reported estimates of repeatability of .45 to .55. A recent study by Dematawewa and Berger (1998) reported repeatability for milk not adjusted for maturity of 0.42 from 122,715 records of up to nine lactations. It is also well documented that some parities are more highly related to other parities (i.e., first parity with second, second with third). Hansen et al (1983) reported a range of estimates of repeatability of first and second parity of 0.40 to 0.61. Swalve and Van Vleck (1987) found that estimates of repeatability for adjacent parities were higher than those that are not adjacent. The average repeatability estimates from the same study were 0.57 for first and second, 0.52 for first and third, and 0.645 for second and third parities. A similar pattern was observed by Dematawewa and Berger (1998).

Genetic correlation between parities

Genetic correlations between parities indicate whether a trait expressed in earlier parities is genetically similar to trait expressed in later parities. They follow the same pattern as repeatability. Swalve and Van Vleck (1987) obtained high genetic correlations for milk production of 0.857, 0.847, and 0.873 for first and second, first and third, and second and third parities. Similarly high genetic correlations were reported by Short et al.

(1990). In the same study, Short et al. (1990) showed a general trend for the genetic correlation between first and second parities to increases with increasing standard deviation of production. Raheja et al. (1989), however, reported lower genetic correlations from Ontario Holsteins. Their estimates were 0.42 for first and second parities, 0.21 for first and third parities, and 0.31 for second and third parities. Again, different estimation procedure may cause this large difference in results.

Estimates from Hot Climate Regions

There are no estimates of genetic parameters for Holsteins in Saudi Arabia in the literature. However, estimates from neighboring countries or countries with similar climatic conditions are available. Fimland et al. (1972), working with data from Israeli Friesians, obtained heritability estimates of 0.22, and 0.18 for first and second lactation. Weller (1989), however, reported lower estimates of heritability of 0.135 and 0.125 estimated from 91,770 records of Israeli Holsteins for first and second lactation. In a later study using even more data from Israeli Holsteins and an animal model, Weller and Ezra (1997) reported a heritability estimate of 0.251. A higher heritability estimate of 0.35 for first lactation has been documented for Holsteins in Zimbabwe (Makuza et al., 1996). The repeatability estimate from the same study for Holsteins in Zimbabwe was 0.35, lower than what is in the literature.

Genetic Parameters for Fertility Traits

Heritability

It has long being known that heritability of most reproductive traits is low, ranging from 0 to 0.1. However, several studies have shown that fertility traits are

moderately heritable. Philipsson (1981) suggested that low heritability may be due to reduction of genetic variance attributed to natural selection. Another reason the author proposed in the same study to explain low heritability was non-additive genetic effects which are not heritable, but known to affect reproductive performance. Weller and Ron (1992) suggested that low heritability estimates of fertility traits may be due to inaccurate estimation of genetic components of fertility. Maijala (1976) and Maijala (1978) reviewed the literature and concluded that despite low heritability of reproductive traits, there is probably considerable additive genetic variation for these traits. Kragelund et al. (1979) suggested that although heritability is low, there is still an opportunity to prevent deterioration in fertility. Based on low heritability for reproductive traits, many researchers concluded that selection on fertility traits would not be beneficial and would be at the expense of milk production, given the unfavorable relationship between milk production and fertility (Hansen et al., 1983; Legates, 1954; Schaeffer and Henderson, 1972). Others (i.e., Freeman, 1984 and Raheja et al., 1989a) see an opportunity for selection for fertility traits if sire evaluation for these traits is based on large numbers of daughters.

Hansen et al. (1983a) studied several measures of fertility traits and their relationship with several production traits using a large data set from New York herds for the first three parities. They reported heritabilities ranging from 0.0 to 0.03. Heritability estimates for calving interval and days open reported by Simeral et al. (1992) were essentially zero. Dong and Van Vleck (1989), however, obtained a higher heritability estimate of 0.15 for calving interval from REML with an animal model. Simeral et al. (1991) also found high heritability estimates for gestation length of 0.24, and 0.43 for age

at first calving. Lee (1976) obtained a heritability of 0.34 for age at first calving using Canadian records on Holstein cows.

Hansen et al (1983) restricted number of services to a maximum of 3 and a maximum of 20 services. They reported higher heritability when the trait was restricted to 3 services in first lactation. Recent work in this area (Dematawewa and Berger, 1998) found heritability estimates of .042 for days open and .028 for number of services per conception from across-parity analyses but a range from .1 to .17 for the same traits in different parities. Marti and Funk (1994) obtained heritabilities of less than .05 for days open in the four production groups studied. Berger et al. (1981) estimated heritability for several production and reproductive traits in different parities. Heritabilities for days open and number of services per conception were low but were higher in later parities. Heritabilities for days open were .02 for first, .03 for second, and .05 for third parity. Heritabilities for number of services were .01 for first, .01 for second, and .06 for third parity. Short et al. (1990) reported greater heritabilities of calving interval in second than in first parity for eight of the nine subsets from grade Holstein cows. Campos et al. (1994), using data from Holsteins in Florida with an animal model, reported heritability estimates of .052 for days open and .098 for calving interval. El amin et al. (1986) evaluated data of Holstein crosses from Sudan and reported heritability estimates of 0.0 for calving interval and days open and .07 for number of services per conception and gestation length. Kragelund et al. (1979), using data from Israeli Friesians, found a heritability of .06 for days open. Weller (1989), using records from Israeli Holsteins, obtained a higher heritability estimate of conception index (the inverse of the number of inseminations to conception) in first (.035) than in second parity (.022). Working with a larger data set, Weller and Ezra (1997), however, reported higher heritability of

conception index in second (.028) than in first parity (.017). Makuza and McDaniel (1996), using data from Zimbabwe, investigated the effect of current and previous days open on milk production. Heritabilities for current days open were .01 in first, .01 in second, and .02 in third lactation. Heritabilities for previous days open were .01 in second and 0.04 in third parity.

Repeatability

Repeatability usually reflects the importance of the individuality of a cow or, in other words, individual variability (Maijala, 1976). In his review, Maijala (1976) reported repeatability estimates of various fertility traits. Repeatability estimates ranged from .03 to .29. Average repeatability estimates for calving interval from 6 studies were .13 and for number of services per conception from 8 studies were .076. Similar values were reported by Dematawewa and Berger (1998) for days open (.115) and for number of services per conception (.083). Badinga et al (1984) reported higher estimates for number of services per conceptions (.20) and days open (.30). Using a large data set of Canadian Holstein, Hayes et al (1992) obtained repeatabilities of .096 for days open and .071 for number of services per conception. Silva et al (1992), using data from Florida for over a 52-year period, reported repeatability of .12 for days open and 0.10 for calving interval. El amin et al. (1986) obtained repeatabilies of 0.14 for gestation length, 0.07 for number of services per conception, .10 for calving interval, and .07 for days open from records on Holstein crosses in the Sudan.

CHAPTER 3

MATERIALS AND METHODS

Climate and Management

Hot dry summers and cool drier winters characterize the climate in Saudi Arabia . Daily temperatures range between 24° C and 53° C during the summer months and –1° C and 20° C during winter months (Rayan and Boland, 1991). June and July are the warmest months and December and January the coolest months. Rainfall is low and variable from year to year. Except in a few months in winter, high temperatures combined with high dry winds and solar radiation generate stressful conditions for milk producing cows.

Management of livestock in arid and semiarid countries is influenced by factors different from those in temperate environments. Because of the harsh environment and scarcity of improved pastures, all dairy farms in the kingdom are intensive dairy operations. In most of these enterprises, the herd consists of straightbred temperate breeds of dairy cattle, especially Holsteins, and large quantities of concentrate and good roughages such as alfalfa and other high quality grasses are used to buffer the environment.

Production Data

Approximately 66,000 records for twice daily milking, 305-d, mature-equivalent milk (ME) yield and reproductive performance of Holstein cows were available from six large

farms located in the central region of the Kingdom of Saudi Arabia. The records available were those of cows calved between 1990 and 1998, allowing for some cows to have more than eight normal parities. The cows in the kingdom were not grazed on pasture but received high concentrate rations two times daily in the lots and during milking. In addition, high quality roughages such as fresh or dried Alfalfa and Rouhdas grass were provided twice daily.

First the Saudi data was edited such that all records of a cow were discarded if she had a missing or an invalid sire identification number (i.e., sire name was not considered unique), and (or) if breed of sire was not Holstein. Sires of cows were identified and then sent to Dairy Records Management System, Raleigh, North Carolina to obtain performance records of daughters of the same sires in the United States. Approximately 916,000 records for ME of Holstein cows that calved in the United State between 1990 and 1998 were provided, of which some had reproductive performance records. Some of the sires in the Saudi data were not represented in the data obtained by the processing center, and some of those records obtained from the processing center were for daughters of sires that were not represented in the kingdom. However, since those sires were related to the sires in the Saudi data, their information was used to increase accuracy of prediction. The data files from both countries were merged to form a composite data file with records of up to eight lactations for some cows.

Several edits were applied to the data file. Because of their reduced value in estimating genetic merit, and because most everything to be learned about an animal's producing ability will be known from the first five lactations, all lactation records after the fifth were excluded. Cows were required to have a sequential data pattern to be

included in the analysis (i.e., if the third record is to be used, first and second records should be available). If any of a cow's previous records were missing, then all her records were eliminated. This helped to overcome the problem of selection or culling of heifers based on their first lactation record. Any duplicate records and all of a cow's records succeeding the duplicate record were eliminated so that the last record for that cow was the record preceding the duplicate record. To reduce the data file to a computationally manageable size, records and herds had to comply with other criteria. All production records were restricted to at least 240 days of milking regardless of milk yield, and herds chosen from the overall data contained 230 cows or more. Those last edits decreased the USA data to approximately 540,000 records but did not significantly reduce the Saudi data.

The calendar year was divided into six calving seasons, two months each, and each season was identified separately for first and multiple calving cows to prevent biases that may be due to different management within a herd based on age or time of freshening. Herd-year-seasons were required to have at least five observations. The last edit reduced the data file to a total of 40,271 cows with 85,060 milk production records, 20,815 cows with 46,777 records from the Saudi data and 19,456 cows with 38,293 records from the United States data (Table 1). In the Saudi data, 7,863 cows had only one record, 5,299 had two records, 3,893 had three records, 2,163 cows had four records, and 1,597 cows had five records. The corresponding numbers from the United States data were 9,241 with only one record, 4,517 with two records, 3,451 with three records, 1,570 with four records, and 677 with five records. Forty-seven percent of the cows in the United States data were in their first lactation, while only 17% of the cows

Table 1. Summary of the data structure for mature equivalent milk yield by parity in Saudi Arabia and the United States.

	Lactation number						
	First	Second	Third	Fourth	Fifth	Total[1]	Total[2]
Saudi Arabia:							
Number of sires	255	242	198	160	107	255	-------
Number of cows	20,815	12,862	7,636	3,769	1,695	20,815	46,777
Number of HYS[3]	193	183	179	161	128	376	-------
United States:							
Number of sires	176	155	152	127	87	176	-------
Number of cows	19,456	10,215	5,698	2,247	677	19,456	38,293
Number of HYS	1,525	1,100	990	639	283	2,640	-------

[1]Total number of unique sire, cow (records), or HYS.
[2]Total number of records.
[3]Herd-Year-Season.

in the Saudi data were in their first lactation. Cows from the Saudi data averaged 2.25 records per cow, and cows from the United States averaged approximately 2 records per cow. Two hundred-fifty five sires were represented in the Saudi data and 176 in the USA data (Table 1) of which 151 sires were common to both countries. The average number of daughters per common sire was 260 in the Saudi data and 246 in the United States data. The average number of daughters for the remaining 104 sires in the Saudi data was 72 and 42 for the remaining 25 sires in the United States data.

Reproduction Data

Reproductive measures that were investigated in Saudi Arabia were calving interval (CI), days open (DO), gestation length (GL), age at calving (AC), and number of services per conception (NS). Those measures were based on actual reproductive records available in the data files. All cows from the Saudi data that were included in the analysis of reproductive traits had these measures of reproduction (i.e., number of observations for all five reproductive traits were the same). Because reproductive measurements were not reported completely, and because the best reported herds were those that were used for the yield data, the reproductive records considered were those records associated with the first four parities of the previously described yield data. However, due to incomplete recording and in order to get the most advantage from the records available, cows were not required to have a sequential data pattern to be included in the analysis of reproductive traits.

Reproductive performance information was more frequently reported in the Saudi data than the United States data. Therefore, only calving interval, gestation length, and

age at first calving were investigated for genotype by environment interaction. In addition, not all cows from the United States data that were included in the reproduction analysis had all three reproductive measures reported (i.e., numbers of observations for the three reproductive traits were different). Observations of days open and number of services per conception was few in the United States data, and were, therefore, not included in the genotype by environment interaction analysis.

To avoid overly influential observations, distribution histograms were created for each reproductive trait to identify the cut off points for the data to be included in the analysis. Restricted limits for calving interval were 300 to 575 days and for days open were 40 to 300 days. Number of services was defined as the total number of breedings during each lactation and was restricted to ten. For the records of gestation length to be included in the analysis, they were required to be at least 265 days from successful insemination to calving date. Records having more than 295 days were discarded. Age at first calving was restricted to a minimum of 22 months. No upper limit was set for age at first calving. Numbers of remaining cows, sires, herd-year-seasons, and records available for the analysis of reproductive traits are listed in Table 2. Distribution of records for milk yield and fertility traits by season is presented in table 3.

Statistical Analysis

Following the suggestion of Dr. Van Vleck (personal communication), the Saudi data were first analyzed using a single-trait, multiple random components animal model to investigate wither the effect of sire by herd interaction was large enough to be included in the multi-trait model. The suggestion was to include this interaction effect if the

Table 2. Summary of the data structure for reproductive traits by parity in Saudi Arabia and the United States.

	Lactation number					
	First	Second	Third	Fourth	Total[1]	Total[2]
Saudi Arabia:						
All reproductive traits[3]						
Number of sires	217	196	187	116	251	-------
Number of cows	14,438	8,763	4,852	2,243	16,108	32296
Number of HYS[4]	143	153	187	141	299	-------
United States:						
Gestation length						
Number of sires	131	140	130	155	155	-------
Number of cows	4,839	5,089	2,643	1130	7,730	13701
Number of HYS	473	643	587	423	1,124	-------
Calving interval and Age at calving						
Number of sires	150	144	130	109	160	-------
Number of cows	9,073	5,375	2,781	1,194	9,998	18,423
Number of HYS	783	654	597	440	1,434	

[1]Total number of unique sire, cow (records), or HYS.
[2]Total number of records.
[3]Reproductive traits in the Saudi data file were gestation length, days open, calving interval, age at calving, and number of services per conception.
[4]Herd-Year-Season.

Table 3. Summary of the data structure for milk yield and fertility traits[1] by season for first and multiple calving cows in Saudi Arabia data set.

Season	Milk Yield		Fertility Traits	
	First calving	Multiple calving	First calving	Multiple calving
January-February	4226	4626	3116	3175
March-April	4705	4597	3468	3445
May-June	2895	3696	1886	2286
July-August	4251	4647	2713	2376
September-October	3278	4597	2104	2289
November-December	1460	3799	1151	2287

Fertility traits are Days open, gestation length, calving interval, age at first calving, and number of services per conception.

proportion of the total variation attributed to this effect is more than 2%. Otherwise it can be ignored. The model included mature equivalent milk yield as the dependent variable, herd-year-season as fixed effects, and sire by herd interaction, animal, permanent environment, and residual as random effects. The magnitude of the effect of the interaction of sire by herd was less than 1%, so this effect was not important enough to be considered under Saudi conditions.

I used the following single-trait and multi-trait animal models to study mature equivalent milk in first and all lactations to obtain components of variances and (co)variances within each country and across the two environments and to study the relation between mature equivalent milk and reproductive traits within and between parities in Saudi Arabia. Milk yields and reproductive traits in the Saudi Arabia and the United States were treated as separate traits in joint analyses. Genetic (co)variances and residual variance components were estimated simultaneously. Estimates of genetic correlations were restricted to the same traits across countries (e.g., milk in Saudi Arabia with milk in the United States, but not milk in Saudi Arabia with calving interval in the United States).

First model. In this model I used single-trait repeated records animal-model from Method R procedure as described by Reverter et al. (1994) to analyze the mature equivalent milk within each country in all available lactations up to five lactations. Method R produces estimates of variances from which genetic, environment, and phenotypic parameters can be derived. The model components included herd-year-season as a fixed effect. Random effects included an animal random additive direct genetic effect, permanent environment, and residual. The Method-R procedure used 500 iterations to reach a convergence precision of $1x10^{-5}$.

Second model. I used this model to analyzed mature equivalent milk yield from first lactation from both countries using a multi-trait (two-trait) animal-model Method R procedure. The components of the joint first-lactation multi-trait analysis were herd-year-season as a fixed effect. Random effects included residual and animal random additive direct genetic effect. The starting genetic and environmental variance values for this model were from the within-country univariate analysis. The genetic covariance value was from Stanton et al. (1990). Because the observations were on different animals, no environmental covariance was expected.

Third model. I estimated variance and covariance for mature equivalent milk yield from all available lactations up to five lactations from both countries using multi-trait (two-trait) animal-model Method R procedure with repeated measurements. In addition to the model components for the joint first-lactation analyses, a permanent environment effect was added to this model. I obtained the starting values for genetic, environmental, and permanent environment variances from within-country analyses and the genetic covariance from joint first-lactation analyses.

Calving interval and gestation length were investigated across the two countries using the information available from all lactations up to four lactations. I used the third model to analyze these traits. The model components included herd-year-season and lactation number as a fixed effects. Random effects included an animal random additive genetic effect, permanent environment, and residual. I analyzed age at first calving using the second model with similar components. Because the number of records available on days open and number of services per conception was small, I only studied gestation

length, calving interval, and age at first calving in the joint analysis between environments.

To study the relation between yield in first three lactations in Saudi Arabia, I used the second model with similar effects to obtain variance and covariance components from pairwise analyses (three analyses). When dealing with milk production in different parities, performance in each parity was considered a different trait. To investigate if a cow's milk yield performance under the Saudi environment on any early lactation is of use in predicting her performance on a later lactation, I analyzed milk yield in different lactations using model one.

I used the third model to analyze the Saudi data to obtain genetic, environmental, and phenotypic correlations between production and reproductive traits across the four lactations (four analyses). Herd-year-season was the fixed effect on milk yield. Fixed effects on reproductive traits were heard-year-season and lactation number. Random effects similar to those in the Third model. I used the second model to obtain genetic and phenotypic (co)variances between milk yield and fertility traits in the same parity for the first three lactations (twelve analyses). In last two analyses, traits were on the same animal, thus environmental covariances existed.

To create the relationship matrix, cow, sire of cow, dam of cow, dam of sire, and sire of sire were extracted from the data file and were stored in a pedigree file. In addition, sire of dam and dam of dam were added to the pedigree file if they were available. Except for dam of cow and dam of dam, most of these sources of information were completely reported. Some sires of dam were missing. The inverse numerator relationship matrix was created using the AINV tool of the Animal Breeder's Tool Kit

(Golden et al., 1992). Numbers of animals in the relationship matrices for all analyses are presented in Table 4.

Once the variance components were estimated, heritability was calculated as the proportion of the phenotypic variance that was attributed to the variation in the additive genetic component. Repeatability was calculated as the proportion of the phenotypic variance that is due to additive and permanent environment variances.

Solution for sires for mature equivalent milk yield in joint first and all lactations were obtained by using the tkblup software program by (Golden, unpublished). The variance components used in tkblup were results from the Method R software "ds6".

Statistical Model

The first model, used for single-trait (within-country) analyses and to obtain repeatabilities between pairwise lactations of first three lactations in Saudi Arabia was

$$\mathbf{Y_{ikl}} = \mu + \mathbf{HYS_i} + \mathbf{A_k} + \mathbf{Pe_k} + \mathbf{e_{ikl}}$$

where

Y_{ikl} = The l^{th} record for cow k of mature equivalent milk production,

HYS_i = the fixed effect due to the i^{th} herd-year-season of freshening,

A_k = the random additive genetic effect due to animal k,

Pe_k = the permanent environment due to cow k, and

e_{ikl} = the random residual effect for the l^{th} record of animal k in HYS i,

Table 4. Number of sires, cows, and number of animals in the numerator relationship matrix in each analysis.

Analysis	Number of sire	Number of cows	Number of animals in A^{-1}
G X E interaction			
First-lactation	327	4,0271	77,434
All-lactation	327	4,0271	77,434
Gestation length	267	2,3838	48,136
Calving interval	270	2,6106	52,275
Age at first calving	270	2,6106	52,275
Saudi Arabia			
Milk yield			
First lactation	255	20,815	40,281
Second lactation	242	12,862	26,786
Third lactation	198	7,636	16,789
Fertility[1]			
All lactations[2]	251	16,108	32,626
First lactation	217	14,438	30,626
Second lactation	196	8,763	19,308
Third lactation	187	4,852	10,874

[1]Fertility traits from Saudi Arabia data set are days open, gestation length, calving interval, age at first calving, and number of services per conception.
[2]Age at first calving is not included.

The first model may be summarized in matrix notation as

$$\mathbf{Y = Xb + Zu + Wpe + e}$$

where

Y is a vector of observations for production variables,

b is a vector of fixed effects for HYS,

u is a vector of additive genetic values of individual animals for the trait or traits considered,

pe is a vector of random permanent environmental effect,

e is a vector of residual effects, and

X, Z, and W are known incidence matrices that assign fixed,, additive random, and permanent effects to records in Y

The mixed model equations (MME) for the first model were

$$\begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + A^{-1}\lambda & Z'W \\ W'X & W'Z & W'W + I_1\gamma \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \\ \hat{pe} \end{bmatrix} = \begin{bmatrix} X'Y \\ Z'Y \\ W'Y \end{bmatrix}$$

$$\mathbf{E} \begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \mathbf{Var} \begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_u & 0 & 0 \\ 0 & I_1\sigma^2_{pe} & 0 \\ 0 & 0 & I_2\sigma^2_e \end{bmatrix}$$

where

A = numerator relationship matrix

σ^2_u = additive variance

σ^2_{pe} = permanent environment variance

σ^2_e = residual variance

$I_{1,2}$ = Identity matrix 1 for cows with records, 2 for all animals in A

$\lambda = \sigma^2_e / \sigma^2_u$ *and* $\gamma = \sigma^2_e / \sigma^2_{pe}$

The second model, used for multi-trait analyses of the first-lactation milk yield across environments, mature equivalent milk yield in different parity, mature equivalent milk and reproductive traits in each one of first three parities in Saudi Arabia, was

$$\mathbf{Y_{ikl}} = \mu + \mathbf{HYS_i} + \mathbf{A_k} + \mathbf{e_{ikl}}$$

where

Y_{ikl} = The l^{th} record for cow k of mature equivalent milk production or calving interval or days open or gestation length or number of services per conception or age at first calving,

HYS_i = the fixed effect due to the i^{th} herd-year-season of freshening,

A_k = the random additive genetic effect due to animal k, and

e_{ikl} = the random residual effect for the l^{th} record of animal k in HYS i,

The second model may be summarized in matrix notation as

$$\mathbf{Y = Xb + Zu + e}$$

where

Y is a vector of observations for production or reproduction variables,

b is a vector of fixed effects for HYS,

u is a vector of additive genetic values of individual animals for the trait or trait considered,

e is a vector of residual effects,

and

X and Z are known incidence matrices that assign fixed and random effects to records in Y

The mixed model equations (MME) for the second model were

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'Y \\ Z'Y \end{bmatrix}$$

where

$$X = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}, \quad Z = \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix},$$

$$Y = \begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix}, \quad \hat{b} = \begin{bmatrix} \hat{b}_1 \\ \hat{b}_2 \end{bmatrix}, \quad \hat{u} = \begin{bmatrix} \hat{u}_1 \\ \hat{u}_2 \end{bmatrix}, \quad e = \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

$$\text{var} \begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 \\ 0 & 0 & r_{11} & r_{12} \\ 0 & 0 & r_{21} & r_{22} \end{bmatrix}$$

where

g_{ij} are elements of G, the additive genetic variance and covariance matrix for animal effects, defined as below:

g_{11} = additive genetic variance for direct effect for trait 1

$g_{12} = g_{21}$ additive genetic covariance between trait 1 and 2

g_{22} = additive genetic variance for direct effect for trait 2

r_{ij} elements of R, variance covariance matrix for residual effects. For the joint first-lactation analysis $r_{12} = r_{21} = 0$,

u and e is just as defined in the first model,

and the rest of the elements are defined as in the first analysis.

The third model is similar to the second model with addition of a random effect of permanent environment for milk analyses. If the analysis includes a fertility trait, lactation number is also added as a fixed effect.

CHAPTER 4

RESULTS AND DISCUSSION

Descriptive Statistics

Phenotypic means and standard deviations for milk yield and measures of fertility for different parities are listed in Table 5. Means increased from first to second parity for milk yield and declined slightly thereafter in both countries. Cows reached their potential production at about 34 to 41 months of age in both countries. Most studies in temperate areas showed steady increase in milk production up to fourth or fifth lactations and decline thereafter. Romero (1986) reported a decline in milk and fat production after the second lactation from Holstein records in Puerto Rico. Means indicate yield was high and the difference in production between countries was relatively small (mean yield from Saudi Arabia was 95% of that in the United States). There was a trend of increasing variation (SD) with advancing parturitions in Saudi data, which was the opposite of the United States data. Because all records for any cow in this analysis were required to be sequential (i.e., if a cow has three records, first and second records should not be missing), culling based on first lactation was not an issue and may not be considered as the reason for the change in genetic variances between first and all lactations. While only 34% of the cows that had a first lactation in the Saudi data did not have a second lactation record, the corresponding percentage for the individuals in the United States data was 51%, implying that more first lactation cows were in the United States data. Averages for gestation length were identical in both countries, but calving intervals in the United

Table 5. Mean and standard deviations for production and fertility traits in Saudi Arabia and the United States in different lactations.

Trait		Lactation number 1	2	3	4	5	Overall
Saudi Arabia:							
ME Milk yield (kg)	Mean	10,381	11,357	11,331	11,162	11,131	10,895
	SD	1,484	1,724	1,824	1,954	2,018	1,735
Days open (days)	Mean	108	105	102	104	-------	106
	SD	53	52	50	51	-------	52
Gestation length (days)	Mean	278	279	280	280	-------	279
	SD	4.6	5	5.1	5	-------	4.8
Calving interval (days)	Mean	387	385	383	384	-------	386
	SD	53	52	50	51	-------	52
Age at calving (months)	Mean	25.5	38.1	50.3	-------	-------	--------
	SD	1.8	2.7	3.3	-------	-------	--------
Number of services	Mean	1.42	2.27	2.25	2.27	-------	1.86
	SD	0.9	1.7	1.6	1.6	-------	1.4
United States:							
ME Milk yield (kg)	Mean	11,390	11,801	11,527	11,234	10,973	11,504
	SD	2,145	2,129	2,004	1,934	1,921	2,114
Gestation length (days)	Mean	278	279	280	280	-------	278
	SD	5	5.3	5.1	5.3	-------	7.2
Calving Interval (days)	Mean	402	400	399	399	-------	402
	SD	63	60	59	59		61
Age at calving (months)	Mean	25.5	38.6	51.4	-------	-------	--------
	SD	3.1	4.25	5.2	-------	-------	--------

States were 15 days on average longer than those in Saudi Arabia in all three lactations. Although means for measures of fertility were similar across parities in both countries, means for calving interval tended to decrease and means for gestation length tended to increase as lactations advance. Mansour (1992) studied reproductive performance with 3,031 records of 1,400 Holstein cows in Saudi Arabia. The average number of services per conception in this study was 1.86 which is similar to the mean of 1.68 reported by Mansour (1992), but averages of days open (106 days), calving interval (386 days), and age at first calving (25.5 months) in Saudi Arabia in our study were shorter than the 120, 398, and 893 days, respectively, reported by Mansour (1992). However, our study is more representative because it utilized 30,296 records for 16,108 Holstein cows. Mansour (1992) reported a mean gestation length of 278 days, and Rayan and Boland (1991) reported a mean of 277.5 days for Holstein in Saudi Arabia, both are similar to the overall average in our study (279 days). Means of fertility traits in Saudi Arabia are comparable to the range of Holstein means in temperate areas (Dong and Van Vleck; 1989, Hansen et al., 1983a; Hayes et al., 1992; Moore et al., 1992; Olds et al., 1979; Raheja et al., 1989b; Ray et al., 1992; Simerl et al., 1992).

Within-Country Analysis

Because the emphasis of this study was primarily on milk, only milk yield was analyzed separately within each country. Minimum, maximum, median, mean, and standard error of the mean of the estimates of genetic, permanent environment, environmental, and phenotypic variation for milk yield in the first five lactations are listed in Table 6. The minimum, maximum, and median estimates of different variance

components do not necessarily correspond to the same sample. Instead they are the values of those parameters from the different subsamples generated by Method R procedure. Estimate of genetic variance for Saudi Arabia was 2/3 the genetic variance for the United States. However, environmental variance for Saudi Arabia was not considerably smaller (85%) than that for the United States. The heritability estimate of milk yield in the Saudi population (0.29) was smaller than the estimate for the United States data set (0.36). This can be attributed to the fact that additive genetic variance in the Saudi data set was reduced relatively more than the residual variance.

Coefficients of additive genetic variation (ACV%, Table 6) were calculated by dividing genetic standard deviations by means. The range of coefficients was 6.7 to 7.8% for the Saudi data and 8.2 to 10.2% for the United States data, implying that animals in the United States express more genetic variation relative to the phenotypic mean. It is possible that the smaller additive genetic variance in the Saudi population is due to environmental conditions related to heat stress during most of the year that prevent the genetic potential of superior individuals from being expressed, therefore restricting differences in milk production between cows with different genetic values.

The ranges of heritability for both countries were similar to the range of 0.18 to 0.51 reported by Van Tassell et al. (1999) using Method R procedures. The heritability estimate for the Saudi data was slightly larger than the estimate of 0.25 by Weller and Ezra (1997) for Israeli Holsteins and was smaller than the estimate of 0.44 by Misztal et al. (1992) and the estimate of 0.50 of Pryce et al. (2000), but was consistent with reported estimates for Holsteins in the literature (Chauhan and Hayes, 1991; Dejager and Kennedy; 1987, Meinert et al., 1989; Miglior et al., 1995). The heritability estimate of (0.29) for Saudi Arabia implies that there is enough genetic variation for milk production

Table 6. Estimates of variance components, heritability (h^2), repeatability(r), additive coefficient of variation (ACV%), and standard errors (SE) for milk yield from within-country analyses for Saudi Arabia and United States in all lactations.

	Variances[1]				Parameters		
	A	PE	E	P	h^2	r	ACV%
Saudi Arabia:							
Minimum	601,047	330,203	1,109,590	2,128,928	.26	.45	6.7
Maximum	796,545	532,126	1,305,740	2,497,202	.33	.49	7.8
Median	672,984	438,869	1,257,800	2,345,377	.29	.48	7.1
Mean	681,050	443,216	1,250,475	2,374,742	.29	.47	7.2
SE	2,787	2,260	2,237	4,247	.001	.0004	.0008
United States:							
Minimum	889,425	248,181	1,280,130	2,601,118	.30	.47	8.2
Maximum	1,369,540	532,826	1,530,900	3,168,226	.43	.54	10.2
Median	1,074,375	355,311	1,478,280	2,918,951	.36	.50	9.0
Mean	1,066,176	385,975	1,470,548	2,922,699	.36	.50	9.0
SE	10,603	6,942	5,550	11,265	.003	.0008	.0004

[1]A=Additive variance, PE=Permanent environment variance, E=Environmental variance, and P=Phenotypic variance.

under Saudi Arabia environmental conditions for improvement in milk yield to be attained by selection.

The permanent environmental variance for the United States data set was 80% that for the Saudi data which compensates for the reduction in genetic variance from the Saudi data and resulted in estimates of repeatability in both countries that are virtually the same (the median estimates were 0.48 for Saudi Arabia and 0.50 for the United States). These values are consistent with the estimate by Van Tassell (1999) who reported repeatability estimates of 0.50 using Method R procedures. Our estimate is also within the range of reports in the literature using different procedures. (Dematawewa and Berger, 1998, Makuza and McDaniel, 1996, Marti and Funk, 1994, Abubakar et al., 1986, Romero, 1986), implying that the likelihood of Holstein cows performing under Saudi environmental conditions to persist in their productivity in advanced lactations is as great as in other areas. Hence, it seems there is a considerable potential for cow selection to improve milk production in Saudi Arabia, and culling on the basis of first lactation records should be effective.

Median and mean heritability and repeatability estimates for the United States data set were 0.36 and 0.50. The heritability estimate was almost double the heritability estimate of 0.196 reported by Dematawewa and Berger (1998) but was in the range of other estimates (Albuquerque et al., 1998; Campos et al., 1994; Van Vleck et al., 1988; and Van Vleck and Dong, 1988).

Joint Analysis Between the United States and Saudi Arabia

Mature Equivalent Milk.

Parameters for variance components, heritability, and genetic correlation estimates from 20 subsamples of Method R for mature equivalent first lactation milk

yield are listed in Table 7. The same genetic parameters and repeatability estimates from joint analysis for mature equivalent milk yield in all lactations are listed in Table 8. The range of genetic variance from those 20 subsamples for the Saudi data was smaller than that of the United States, but median, mean, and coefficients of estimated genetic variance (641,391 kg2, 642,398 kg^2, and 7.7%, respectively) for Saudi Arabia did not differ from those (631,668 kg^2, 643,525 kg^2, and 7.0%, respectively) for the United States. However, due to the environmental constraints that affect the performance of individuals under a Saudi environment and the fact that these data were drawn from a small number of large-scale farms, estimates of residual variance for Saudi Arabia were smaller than estimate for the United States. The median estimated residual variance for Saudi Arabia was 79% that of the United States. The range of residual variances from those 20 subsamples (1,445,580 to 1,727,080 kg^2) for Saudi Arabia was less than half that of the United States (1,674,200 to 2,277,600 kg^2) and the maximum estimate for Saudi was similar to the minimum estimate for the United States. Because these changes in genetic and residual variances were disproportional, the estimate of heritability (0.29) for Saudi Arabia was slightly higher than the estimate for the United States (0.24). In the analysis of all lactations, estimates of genetic variance for Saudi Arabia increased and estimates for the United States decreased (Table 8) from those estimates from within-country analyses (Table 6), but differences were small. Also, coefficients of additive genetic variation for the Saudi data set from all lactations analysis increased slightly and coefficients for the United States decreased slightly from the corresponding coefficients from within-country analysis. It is possible to attribute this change in genetic variances to the fact that the breeding values that produce these estimates in both countries are

Table 7. Estimates of variance components[1], heritability (h^2), additive coefficient of variation (ACV%), genetic correlation ($r_{A_{US},A_{SA}}$) and standard errors (SE) for milk yield from joint analysis between Saudi Arabia and United States in first lactation.

	Variances			Parameters		
	A	E	P	h^2	ACV%	$r_{A_{US},A_{SA}}$
Saudi Arabia						
Minimum	569,851	1,445,580	2,028,114	.26	7.3	.25
Maximum	736,608	1,727,080	2,417,409	.33	8.3	.84
Median	641,391	1,553,370	2,195,963	.29	7.7	.68
Mean	642,398	1,557,823	2,200,222	.29	7.7	.60
SE	3,248	6,079	6,553	.11	.0002	.01
United States						
Minimum	425,880	1,674,200	2,184,672	.16	5.7	
Maximum	986,325	2,277,600	2,943,945	.34	8.6	
Median	631,668	1,954,090	2,630,332	.24	7.0	
Mean	643,525	1,961,191	2,604,716	.24	7.0	
SE	11,208	9,390	12,580	.003	.0006	

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.

Table 8. Estimates of variance components[1], heritability (h^2), repeatability (r), additive coefficient of variation (ACV%), genetic correlation ($r_{A_{US},A_{SA}}$) and standard errors (SE) for milk yield from joint analysis between Saudi Arabia and United States in all lactations.

	Variances				Parameters			
	A	PE	E	P	h^2	r	ACV%	$r_{A_{US},A_{SA}}$
Saudi Arabia								
Minimum	671,522	417,996	1,344,020	2,535,697	.24	.45	7.5	.03
Maximum	949,970	607,998	1,554,220	2,915,927	.33	.50	8.9	.38
Median	795,955	488,154	1,435,625	2,719,432	.29	.47	8.0	.17
Mean	798,335	487,194	1,439,878	2,725,408	.29	.47	8.2	.18
SE	3,343	1,913	2,260	4,495	.00	.00	.00	.00
United States								
Minimum	725,801	277,357	1,392,440	2,788,619	.24	.47	7.4	
Maximum	1,319,790	746,645	1,627,120	3,287,506	.42	.52	9.9	
Median	991,195	454,484	1,508,385	3,016,286	.34	.50	8.6	
Mean	1,007,032	479,234	1,508,759	2,995,026	.34	.50	8.7	
SE	6,745	5,426	2,764	5,438	.002	.0005	.007	

[1]A=Additive variance, PE=Permanent environment variance, E=Environmental variance, and P=Phenotypic variance.

positively genetically correlated. Because of this relationship, greater genetic differences among animals (sires in particular) in the United States data could increase the genetic variance between the same animals in Saudi data. For the same reason, a reduction in genetic variation between animals in the United States is expected as a result of reduced genetic variation among the same animals in the Saudi data set. Estimate of residual variances for the Saudi data set from all-lactation joint analyses was also greater than that of within-country analyses; however, the difference was small.

Because the proportion of change in genetic and phenotypic variances was relatively equal in both countries, heritability estimates from both within and across-environment analyses for all lactations were similar. In contrast to the report by Dematawewa and Berger (1998) in which across-parity estimates of heritability decreased compared to the first-parity estimate for a milk yield, median and mean estimates of heritability for the Saudi data remained constant (0.29). Median and mean estimates of heritability for the United States increased from .24 in the first-lactation analysis to .34 in the all-lactation analysis. Substantial differences for additive genetic variance for the United States were revealed between joint first and all-lactations analyses. While the median and mean estimates of phenotypic variance for the United States from across-parity analysis were only 15% greater than those estimates from first lactation analysis, the median and mean estimates of genetic variance from across-parity analysis were 56% greater than those estimates from the first lactation analysis. Dairymen usually select cows based on their first lactation records. This implies that individuals in later lactations are selected genotypes which would be expected to be more uniform resulting in reduced genetic variance and, hence, heritability. However, this is

not the case in this study because, again, the edits of the records in the present study assume no culling (sequential records are required). In fact both genetic and phenotypic variances increased in both countries, but residual variance for the United States in all lactations decreased by an approximately 22% of that in the first lactation. It seems that younger cows are under the stress of production and growing at the same time, but as they get older and approach mature weight, they are more able to express their potential in milk production. Repeatability estimates from joint analysis were similar in both countries and did not differ from those from within-country analysis.

Median and mean estimates of genetic correlations in first and all lactations are listed in Tables 7 and 8. Median and mean estimates from first lactation analysis were moderate (0.68 and 0.60), but estimates from the all-lactation analysis were substantially lower (0.17 and 0.18). This suggests the existence of a significant genotype by environment interaction and a considerable change in rank of sires across environments, because if the genetic correlation is low "then the characters are to a great extent different, and high performance requires a different set of genes" [Falconer, 1993]. It becomes obvious that progeny of some sires selected in temperate areas are more susceptible to heat than progeny of other temperate area's sires. These results agree with those of Abubaker (1985) who investigated the genotype by environment interaction between Mexico and Colombia and reported a considerable interaction between sires and environments as indicated by the rank correlation between sire values of .26. Several studies reported small correlations, suggesting a considerable genotype by environment interaction (Bar Anan et al., 1987; Cunnungham and O'Byrne, 1977; Holmes, 1995, Romero, 1986; Schneeberger et al., 1982). However, for different dairy traits, the

correlations of breeding values for animals performing in different environments were reported by the majority of researchers to be one or close to unity (Carabano et al., 1990; Danell, 1982; Metzger et al., 1994; Syrstad, 1990; Stanton et al., 1991). Using BLUP procedures, breeding values for the 151 Holstein sires with progeny in both countries were calculated. Number of daughters for each sire varied, but was small in general. Of those common sires, 57 sires had 20 daughters or more in each environment. Presented in Tables 9 and 10 are the identification numbers, estimated breeding values, rank, and number of daughters for the top 20 and the bottom 20 sires of those 57 sires in first-lactation milk yield, respectively. Tables 11 and 12 show similar information (plus number of records) for the top and bottom 20 sires in all lactations, respectively. Rank of sires in Table 9 to 12 is based on the ranking of the common 151 sires in each country. Rank correlation was calculated using the "rank" tool as described by Golden et al (1992). Rank correlation for the estimated breeding values for the 57 sires among first and all lactations within Saudi Arabia was .77 and the corresponding correlation within the United States was .80. Though these are less than perfect (unity) correlations, they show how similar milk estimated breeding values are for sires in different periods of their daughters lives and that the same genes are responsible for this trait at different ages.

The rank correlation for the 57 sires between the first lactation in both countries was .44, and the rank in all lactations was .38, suggesting rank of sires did change basedon the environment. In Table 9, the first five top ranking sires of those sires having 20 daughters or more ranked 2^{nd}, 3^{rd}, 6^{th}, 7^{th}, and 8^{th} under the United States environment, but ranked 13^{th}, 50^{th}, 6^{th}, 11^{th}, and 147^{th} under the Saudi environment. Similarly the last five bottom ranking sires ranked 147^{th}, 148^{th}, 149^{th}, 150^{th}, and 151^{st} under the United

Table 9. Estimated breeding values (EBV), number of daughters (ND), and rank of top 20 Sires with 20 daughters or more of the 151 sires common to the United States (US) and Saudi Arabia (SA) from the joint analysis of first-lactation milk yield.

	United States		Saudi Arabia		Rank	
Sire Code	ND	EBV	ND	EBV	US	SA
2027136	35	886	96	605	2	13
1974710	54	875	277	157	3	50
2093626	321	774	332	735	6	6
2010311	73	683	347	686	7	11
2043401	32	683	50	-996	8	147
2021095	244	681	224	268	9	36
2012688	37	505	215	718	12	8
2033717	436	496	699	993	13	3
1919240	43	423	375	184	19	35
1929028	91	406	134	323	20	29
1915805	53	332	76	1,160	24	2
1989712	204	323	626	462	25	19
2048946	23	292	127	-69	28	79
1971523	183	250	191	373	33	23
1875896	309	205	22	108	37	56
1926240	64	202	70	703	38	9
2018440	357	149	633	562	43	15
1882919	41	74	222	316	52	30
1841366	697	61	72	-751	56	138
1892913	812	51	61	140	57	51

Rank correlation = .44

Table 10. Estimated breeding values (EBV), number of daughters (ND), and rank of bottom 20 sires with 20 daughters or more of the 151 sires common to the United States (US) and Saudi Arabia (SA) from the joint analysis of first-lactation milk yield.

	United States		Saudi Arabia		Rank	
Sire Code	ND	EBV	ND	EBV	US	SA
1916401	110	-198	479	-210	100	103
2007818	241	-207	52	595	103	14
1891196	125	-280	248	72	109	63
2009162	69	-305	247	-629	113	131
2058403	86	-318	840	-218	116	104
1924058	88	-332	790	51	118	65
1983304	50	-387	320	500	121	16
2095320	44	-446	202	256	124	39
2010754	116	-539	76	-723	127	137
2020696	95	-565	285	-67	130	78
2048480	27	-572	475	318	132	31
2026916	36	-679	537	-425	137	122
1818156	30	-689	57	-861	139	145
2009359	53	-802	105	-594	143	129
1969877	39	-847	97	436	145	20
2000997	95	-1,042	86	-544	147	124
2014309	20	-1,196	457	-230	148	108
1990589	84	-1,234	580	-630	149	132
2049221	25	-1,287	300	753	150	5
2031088	63	-1,469	139	-898	151	146

Rank correlation = .44

Table 11. Estimated breeding values (EBV), number of daughters (ND), number of records (NR), and rank of top 20 sires with 20 daughters or more of the 151 sires common to the United States (US) and Saudi Arabia (SA) from the joint analysis of all-lactations milk yield.

	United States			Saudi Arabia			Rank	
Sire Code	ND	NR	EBV	ND	NR	EBV	US	SA
2033717	436	871	1,638	699	1,667	892	2	11
2027136	35	60	1,635	96	330	882	3	12
2043401	32	77	1,477	50	125	-150	6	107
2018440	357	774	1,363	633	1,709	540	7	33
2021095	244	395	1,343	224	495	122	8	77
2019222	522	1,063	1,226	623	1,691	197	11	70
2010311	73	105	1,146	347	697	626	12	28
2093626	321	377	1,142	332	665	752	13	18
1842366	697	1,406	983	72	268	-119	16	109
1986558	316	711	968	242	869	1,123	17	8
2048946	23	30	788	127	255	-21	24	90
2012688	37	92	703	215	800	692	28	23
1875896	309	702	579	22	118	-231	32	114
1892913	812	1,799	533	61	326	1,541	36	2
1915805	53	158	496	76	434	1,159	42	6
2059532	276	547	441	98	211	-143	46	106
1920908	91	160	439	134	607	314	47	57
1989712	204	336	377	626	1,503	295	51	59
1926240	64	116	370	70	415	402	52	48
2008547	43	75	342	790	990	-43	55	95

Rank correlation = .38

Table 12. Estimated breeding values (EBV), number of daughters (ND), number of records (NR), and rank of bottom 20 sires with 20 daughters or more of the 151 sires common to the United States (US) and Saudi Arabia (SA) from the joint analysis of all-lactations milk yield.

	United States			Saudi Arabia			Rank	
Sire Code	ND	NR	EBV	ND	NR	EBV	US	SA
2010754	116	254	-126	76	199	-43	92	94
2096865	23	27	-144	94	188	-643	93	136
2095320	44	82	-177	202	410	-231	95	113
2043468	121	219	-272	280	746	-584	103	134
1888783	24	39	-291	209	940	1,175	105	5
1938955	20	47	-352	79	388	-1,007	111	150
2009359	53	142	-384	105	340	-447	115	126
2015271	53	101	-458	144	344	-34	121	93
1969877	39	72	-466	96	269	1,547	122	1
1891196	125	307	-488	248	1,081	1,081	124	104
1983125	28	57	-500	290	290	-272	126	119
1884404	21	33	-594	31	144	974	127	9
2026916	36	85	-746	537	1,407	-700	133	140
1919156	30	66	-757	58	225	-658	134	138
2000996	95	237	-815	86	303	-851	137	146
2014309	20	31	-856	457	914	-453	138	127
1990589	85	155	-971	580	1,937	-550	139	133
1924058	88	187	-1,036	790	2,680	-277	143	63
2031088	63	110	-1,062	139	307	-362	145	123
2049221	25	47	-1,139	300	600	381	147	49

Rank correlation = .38

States environment, but ranked 124th, 108th, 132nd, 5th, and 146th under the Saudi environment (Table 10). It is obvious from these results that if selection of those sires was based on the outcome of the estimated breeding values in the present study, a different set of sires would be selected by Saudi dairy managers because of the genotype by environment interaction. These results indicate that if this interaction is not taken into account by dairymen in Saudi Arabia, then the published sire summaries predicted transmitting abilities (PTA) for those selected sire from the United States would reflect the genetic values for those animals investigated under the more favorable environment but not under harsh Saudi conditions.

Reproductive Traits.

Estimates of variance components for gestation length and calving interval for cows included in the all-lactation joint analysis are presented in Tables 13 and 14, respectively, and estimates for age at first calving for cows in the first-lactation joint analyses are listed in Table 15. Median and mean estimates of phenotypic variance for cows in Saudi Arabia were 35% and 38%, 74% and 72%, and 56% and 45% of those estimates in the United States for gestation length, calving interval, and age at first calving, respectively. The range of the phenotypic variance in the United States was also greater, which can be attributed to the greater environmental variance available under the United States' environment conditions. Because the records are from small number of well managed farms, more environmental uniformity can be seen in the Saudi data. The range of the coefficient of genetic variance is slightly smaller in Saudi Arabia than in the United States. It appears that under relatively good management conditions, less genetic

Table 13. Estimates of variance components[1], heritability (h^2), repeatability (r), additive coefficient of variation (ACV%), and genetic correlation ($r_{A_{US},A_{SA}}$) for gestation length from all-lactation joint analysis between Saudi Arabia and the United States.

	Variance Components				Parameters			
	A	PE	E	P	h^2	r	ACV%	$r_{A_{US},A_{SA}}$
Saudi Arabia								
Minimum	3.6	.07	13	17	.20	.23	.80	.14
Maximum	9	1	29.6	39	.24	.26	1.10	.99
Median	5.7	.30	20	27	.22	.24	.90	.96
Mean	6.0	.45	20	26	.22	.24	.90	.81
SE	.11	.02	.40	.54	.00	.00	.00	.03
United States								
Minimum	1	.80	15.2	172	.03	.10	.40	
Maximum	14.7	5	95.4	112.8	.13	.16	1.30	
Median	5.3	3.40	64	74.6	.07	.12	.80	
Mean	5.88	3.2	60	69	.08	.13	.90	
SE	.31	.10	1.6	2	.00	.00	.00	

[1]A=Additive variance, PE=Permanent environment variance, E=Environmental variance, and P=Phenotypic variance.

Table 14. Estimates of variance components[1], heritability (h^2), repeatability (r), additive coefficient of variation (ACV%), and genetic correlation ($r_{A_{US},A_{SA}}$) for calving interval from all-lactation joint analysis between Saudi Arabia and United States.

	Variance Components				Parameters			
	A	PE	E	P	h^2	r	ACV%	$r_{A_{US},A_{SA}}$
Saudi Arabia								
Minimum	14	57	2,214	2,477	.01	.07	.90	.03
Maximum	8,159	255	2,816	10,513	.78	.80	23	.99
Median	142	137	2,555	2,835	.05	.10	3.10	.99
Mean	571	129	2,527	3,228	.11	.15	4.40	.83
SE	61	2	6.5	59.6	.01	.01	.00	.01
United States								
Minimum	11	76.5	3,057	3,288	.00	.05	.80	
Maximum	15,187	362	3,923	18,827	.80	.81	30	
Median	109	229	3,438	3,824	.08	.09	2.60	
Mean	782	235	3,441	4,459	.08	.14	4.10	
SE	113	2.7	7.6	113	.01	.00	.00	

[1]A=Additive variance, PE=Permanent environment variance, E=Environmental variance, and P=Phenotypic variance.

Table 15. Estimates of variance components[1], heritability (h^2), additive coefficient of variation (ACV%), and genetic correlation ($r_{A_{US},A_{SA}}$) for age at first calving from first lactation joint analysis between Saudi Arabia and the United States.

	Variance			Parameter		
	A	E	P	h^2	ACV%	$r_{A_{US},A_{SA}}$
Saudi Arabia						
Minimum	1.02	.62	1.65	.60	4.0	-.01
Maximum	2.18	1.4	3.60	.66	5.7	.18
Median	1.9	1.13	3.01	.62	5.4	.10
Mean	1.9	1.14	3.0	.62	5.3	.08
SE	.03	.02	.05	.00	.00	.01
United States						
Minimum	.44	2.8	3.40	.04	2.6	
Maximum	1.18	12.1	12.53	.28	4.3	
Median	.60	4.5	5.37	.14	3.0	
Mean	.70	6.03	6.7	.14	3.3	
SE	.02	.32	.31	.01	.00	

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.

variance can be seen for some traits such as fertility. Nevertheless, the proportions of genetic variance were greater and the proportions of environmental variance were smaller for all three traits in the Saudi data than in the United States data, resulting in higher heritabilities for these traits in Saudi Arabia. Coefficients of genetic variation were similar for gestation length and calving interval in both countries, but the coefficient for age at first calving in the United States was 55% of that in Saudi Arabia. The median estimate of heritability for gestation length in Saudi Arabia (0.22) is similar to estimates of .22 and .24 reported by Silva et al. (1992) and Simerl et al. (1991), respectively. However it is larger than the majority of results in the literature, maybe in part due to using a different procedure (i.e., an animal model), or it may be due to incorporating different variables in the model (Dong and van Vleck, 1989).

Everett et al. (1966), using Henderson's method 1, reported heritabilities of calving interval for Holsteins of .08, remarkably in agreement with the median heritability estimates of calving interval of .05 and .08 for Saudi Arabia and the United States in this study, respectively. Other estimates were also reported in this range (from 0.021 to 0.098) by Silva et al. (1992), and Campos et al. (1994). However, our estimates are smaller than those of .17 and .14 reported by Dong and Van Vleck (1989).

The median heritability estimate of .62 for age at first calving in Saudi Arabia undoubtedly represents genetic differences among animals in rate of maturity or it reflects the intention of the Saudi dairymen to bred daughters of some sires whom known to have potential in milk yield earlier than daughters of other sires. Though not as large, high heritability estimates for age at calving were also reported by Allaire and Lin (1980), Lee (1976), and Simerl et al. (1991). However, the estimate in our study is

substantially different from the smaller heritability estimates of .04 and .05 reported by Moore et al. (1992) and Seykora and McDaniel 1983, respectively. The median estimate of age at first calving of .14 attained for the United States in the present study is slightly higher than the estimate of .12 by Hermas et al. (1987) and slightly smaller than the estimate of .16 by Hansen et al (1983b).

Estimates of repeatabilities for gestation length and calving interval in both countries are listed in Tables 12 and 13. Median and mean repeatabilities of gestation length in Saudi data were higher (0.24 and 0.24) than those estimates (0.12 and 0.13) in the United States. Though genetic variances were similar in both countries, phenotypic and permanent environmental variances in the Saudi data set were substantially smaller than those of United States resulting in larger estimates of repeatability. Because permanent environmental variance for Saudi data was small, median and mean repeatabilities and corresponding heritabilities were almost equal, but repeatabilities for the United States data were close to two times the corresponding heritability estimates. Repeatability estimates for gestation length in the Saudi data set were almost twice the estimate reported by El Amin et al. (1986) of .14 for crosses of Holstein, Shorthorn, Ayrshire, and Guernsey with Butana cattle in Sudan.

Median and mean repeatability estimates for calving interval were similar in both countries. Median estimates in Saudi Arabia and the United States were .10 and .9, respectively. Comparative results from the literature for calving interval in temperate areas were consistent with our result. Maijala (1976) reported a weighted average repeatability of .131 from six studies for calving interval. The repeatability estimate of .10 reported by Silva et al. (1992) is similar to the median estimates of both countries in

the present study. It seems that under good management, especially in reducing heat stress and keeping good reproductive records, Holstein cows' reproductive performance in Saudi Arabia is similar to that in temperate areas.

Estimates of genetic correlations between countries for gestation length, calving interval, and age at first calving are presented in Tables 13 through 15. Median genetic correlations for gestation length and calving interval across the two environments were virtually unity (.96 and .99, respectively). Means of estimates were also large (above .80) and the estimates of standard error of the mean were small. This is a strong indicator of the absence of the first type of genetic by environment interaction (i.e., the classic type) in these two traits. Animals (sires) tended to rank similarly in both environments because, as stated by Falconer (1993), "if the genetic correlation is high, then performance in two environments represents very nearly the same character, determined by very nearly the same set of genes." However, scaling effect of the first situation of the heterogeneous variance that leads to the second type of genotype by environment interaction is expected. That is, when genetic variances in both environments are equal but residual variances are different, then the fraction of total variance that can be attributed to genetic variance will vary. Consequently, heritability changes. This is the case for gestation length in our results.

Median and mean genetic correlations between countries for age at first calving were considerably lower (.10 and .08, respectively) than correlations for gestation length and calving interval. The low estimate of genetic correlation is an indicator of the existence of genotype by environment interaction. There were 125 sires common to both countries with age at first calving observations available. The range of estimated

breeding values for age at first calving for those sires was –2.67 to 2.1 months and for cows with records –2.9 to 9.05 months in Saudi Arabia. Corresponding values for sires and cows with records in the United Sates were –.95 to 1.7 months and –.5 to 6.32 months, respectively. Of those 125 common sires, 38 sires had 20 daughters or more in each country. Presented in Table 16 are estimated breeding values, number of daughters, and rank of those 38 sires. Sires in Table 16 ranked differently in each environment. The first three top ranking sires under United States environment ranked 2nd, 3rd, and 4th, but ranked 60th, 13th, and 37th in Saudi Arabia. The correlation between these values should manifest the importance of this reranking. The rank correlation between the 125 sires was very small (r = .11) implying significant reranking. However, the rank correlation for the 38 sires with 20 daughters or more was slightly higher (r = .35).

Genetic Aspects of Milk Production and Reproductive Performance of Holstein in Different Parities Under Saudi Arabian Environment

Milk Production in Different Parities

Heritability.

Table 17 shows estimates of genetic, environmental, and phenotypic variances, and repeatability from pairwise analysis for the first three parities for milk yield in Saudi Arabia. Heritability estimates from univariate analyses are listed in Table 18. Medians of heritability estimates were .29, .26, and .22 for first, second, and third lactations, respectively, which were larger than estimates by Raheja et al. (1989b) and smaller than estimates reported by Swalve and Van Vleck (1987), but were within typically reported ranges (Berger et al., 1981; Damatawewa and Berger, 1998; Fuerst and Solkner, 1994;

Table 16. Estimated breeding values (EBV), number of daughters (ND), and rank of the 38 sires with 20 daughters or more from the 125 sires common to the United States (US) and Saudi Arabia (SA) from the joint analysis of age at first calving.

	US		SA		Rank	
Sire code	ND	EBV	ND	EBV	US	SA
1989712	117	.73	494	.10	2	60
1919240	24	.70	308	1.0	3	13
1926240	28	.62	67	.41	4	37
2020696	42	.53	266	.43	6	34
1916401	28	.43	366	.70	13	24
1938955	20	.39	36	1.32	18	4
2015271	27	.36	133	.27	22	43
1841366	313	.35	24	-1.09	25	100
1990589	40	.34	519	1.0	26	12
1986558	174	.17	210	.38	44	26
1985441	49	.16	224	.38	48	38
1962728	27	.16	88	.71	49	23
1974710	33	.16	258	.21	51	49
2012688	26	.14	181	.87	52	17
1915805	31	.11	60	.87	55	16
2033717	275	.05	449	-.68	64	91
1892913	429	.03	242	1.09	69	8
2058403	27	.02	242	-2.25	70	121
1891196	43	-.00	230	.42	76	35
2009162	37	-.02	218	1.55	78	3
1999661	83	-.08	87	.51	84	30
2093626	85	-.10	34	-2.57	86	123
2030202	57	-.12	320	-.243	88	74
2059532	153	-.13	67	.32	92	41
1983304	25	-.15	297	.44	94	33
2018440	271	-.15	513	.22	95	45
2010754	48	-.16	75	-.21	96	71
2019222	321	-.20	505	-.32	100	80
1882919	36	-.20	99	.52	101	29
2021095	77	-.21	144	-1.23	102	106
2043401	26	-.21	49	.79	103	22
2043468	88	-.32	223	.13	110	57
1971523	65	-.33	120	-.94	111	99
2009359	40	-.41	95	-.76	115	94
2027136	20	-.43	89	1.10	116	7
2000997	61	-.47	84	.26	117	44
2032546	65	-.62	42	-.01	120	67
2095320	21	-.72	49	-2.44	123	122

Rank correlation = .35

Table 17. Estimates of variance components, repeatability, and standard error of the mean (SE) from pairwise analysis for milk yield in the first three parities.

	Variances				
Parities	A	PE	E	P	R
First and Second					
Minimum	440,164	357,751	1,111,650	2,047,866	.44
Maximum	787,725	635,119	1,277,890	2,456,262	.49
Median	565,836	435,998	1,187,720	2,243,035	.47
Mean	576,796	470,908	1,185,664	2,233,369	.47
SE					.00
First and Third					
Minimum	329,556	170,761	1,218,560	1,962,335	.36
Maximum	970,399	562,739	159,920	2,643,480	.43
Median	512,262	367,631	1,452,725	2,371,943	.38
Mean	526,703	381,178	1,435,156	2,343,038	.38
SE					.00
Second and Third					
Minimum	417,391	307,236	1,252,360	2,495,776	.45
Maximum	1,197,730	1,040,400	1,519,080	3,120,932	.56
Median	812,951	547,145	1,391,270	2,804,307	.50
Mean	830,138	581,436	1,382,656	2,794,230	.50
SE					.00

and Miglior et al., 1995). The range of heritability estimates increased and the median and mean of the estimates decreased as parity increased. Low heritabilties in later lactation may be due to decreased genetic variance and increased error variance because of increase of sampling variance associated with fewer observations available on later parities than on earlier parities (Table 1). Selection is not the issue here because of the sequential criteria. Comparative results from the literature are quite contradictory. In agreement with our result, Hansen et al. (1983b), using Henderson Method 3, reported heritabilities of .18, .14, and .10 in first, second, and third parities, respectively. Banos and Shook (1990) also observed a reduction in the heritability as parity increased using models with and without sire by herd interaction. Other studies in the literature report an increase in heritability associated with increase lactation number (Maijala and Hanna, 1974; Powell et al., 1981; Tong et al., 1979). Fuerst and Solkner (1994), Raheja et al. (1989b), and Swalve and Van Vleck (1987) found heritabilities for milk production to be constant over the first three lactations.

Repeatability.

Pairwise estimates of variance components and estimated repeatability for milk yield in Saudi Arabia between the first three parities are presented in Table 17. Medians and means for estimates of repeatability for all pairs of parities were not equal and standard errors of the means were very small. These parameters were .47, .38, and .50, between first and second, first and third, and second and third, respectively. The same trend was reported by Dematawewa and Berger (1998), who obtained repeatability estimates of .377 and .29 between first and second and first and third lactations- estimates

that were lower than the corresponding pairwise parities in the present study. However, repeatability between second and third lactations were the highest as in our findings. It seems that as age advance, permanent environment effects become greater. Dematawewa and Berger (1998) attributed the larger repeatability estimate between second and third than between first and second to a larger proportional reduction in phenotypic variance as compared to additive and permanent environment variances. Their conclusion cannot be supported by the findings in the present study, because phenotypic variance from the models that included third parity increased. The lower repeatability estimate between first and third parities can be attributed to the increased residual variance and reduced variance of producing ability (Table 17). Higher repeatability estimates between adjacent parities is an indication that milk production in one parity is more likely to be repeated in the successive parity than in the nonsuccessive parity under a Saudi environment. Hansen et al (1983) reported a constant repeatability for mature equivalent milk yield between pairs of lactations up to third lactation.

Genetic and Phenotypic Correlations

Median, mean, and standard error of the mean of genetic and phenotypic correlations between milk yields in the first three lactations are listed in Table 18. All genetic correlations were high (>0.85) implying a strong genetic relationship between milk yields in the first three lactations. Medians of genetic correlations were .87, .86, and .93 between first and second, first and third, and second and third, respectively. The trend of lower genetic correlations for those estimates that include first parity has been documented by other studies (Banos and Shook, 1990, Maijala and Hanna, 1974, and

Table 18. Estimates of heritability[1] (on diagonal), genetic correlation (above diagonal), phenotypic correlation (below diagonal), and standard error (SE) between milk yields in first three parities in Saudi Arabia.

	Parities		
	First	Second	Third
First			
Median	.29	.87	.86
Mean	.29	.86	.80
SE	.00	.01	.05
Second			
Median	.44	.26	.93
Mean	.45	.26	.88
SE	.02	.00	.08
Third			
Median	.40	.50	.22
Mean	.40	.50	.22
SE	.01	.03	.00

[1]Heritability is from univariate analysis

Swaleve and Van Vleck, 1987). It was proposed by Maijala and Hanna (1974) that it is possible that milk production is not the same trait in first and later parities. In other words different set of genes affect milk production in different lactations (Banos and Shook, 1990). However, in most animal breeding studies, traits with genetic correlations above .80 are considered highly genetically correlated. Consequently milk production in the first three parities in Saudi Arabia is likely the same trait, animals are expected to rank similarly, and no genetic by environment (parity or age) interaction is to be assumed. This result is supported by the rank correlation of .79 between estimated breeding values from first and all-lactations from Saudi data.

Phenotypic correlations for milk yield in the first three parities were all smaller than genetic correlations. Medians and means of estimated phenotypic correlations ranged from .40 to .50. Following the same trend of genetic correlations, the largest correlation was between second and third lactation and the lowest correlation was between first and third lactation. These estimates were slightly lower than corresponding correlation estimates of 0.57, 0.52, and 0.645 reported by Swalve and Van Vleck (1987) using an animal model.

Reproductive Traits.

Relationships between Reproduction and Production in all Parities

Means and standard deviations for measures of fertility in different parities were presented in Table 5. Relative to parity, fertility means behaved differently from yield means. Means of days open tended to decrease as lactations advanced; however, means for number of services per conception showed a distinctive increase from first to second days later than cows in second, and third lactations, respectively, and had two and four

days longer calving intervals than those cows in second and third parities, respectively. Interpretations of these means were puzzling because cows in first lactation had not yet exposed to the first lactation stress. The work of Hansen et al. (1983) suggests that lactation and became constant thereafter. Cows in first lactation conceived three and sixdaughters from selected sire for high milk yield had improved fertility (i.e., favorable relation between genetic potential and fertility) as heifers but was hindered in first lactation. They suggested that daughters of sires with high potential for yield are growthier or they tend to mature earlier. First-lactation cows needed a smaller number of inseminations per conception than cows in other parities. There were no obvious patterns in the standard deviations for days open, implying that no management practice was exercised to intentionally delay breeding first lactation cows, because if the dairy herd's management did so, the variance of days open in first lactation should be smaller than the variance for later lactations (Berger et al, 1981). Standard deviations were 53, 52, and 50 days for the first three lactations, respectively, indicating no distinct change in variance relative to parity. The mean of days open of 106 days in the present study is substantially lower than the mean of 166 for Holstein in Florida reported by Campos et al. (1994). However, it was slightly larger than the mean of 100 days reported by Kragelund et al. (1979) for Israeli Friesian. The mean for number of services per conception of 1.86 services in this study is smaller than the overall mean of 2.6 services for six strains of European Friesians in Egypt reported by Mostageer (1981). Our estimates are in general agreement with estimates for Holsteins in other studies in temperate areas (Everett et al., 1966; Dematawewa and Berger, 1998; Hayes et al., 1992). Means for gestation length, calving interval, and age at first calving were discussed earlier in the joint analysis for

fertility traits between Saudi Arabia and United States. Because the results are similar in this analysis of reproductive traits for cows from Saudi Arabia to the result from joint analyses and the only change is the slightly proportional decrease in variance component estimates, variance components, heritabilities, repeatabilities, and coefficients of additive genetic variance are presented in Table 19 without comment.

Parameters for estimates of variance components, heritability, repeatability, coefficient of additive genetic variation for days open, gestation length, calving interval, age at first calving, and number of services per conception for cows included in all lactations analysis are presented in Table 19. Results suggest that days open for Holsteins from Saudi Arabia have similar variability when compared to studies in temperate areas (Abdallah and McDaniel, 2000, Dematawewa and Berger, 1998) using an animal model. Almost 90% of the phenotypic variance for days open was due to environmental factors. However, the medians of the coefficient of additive variation of 9% for days open indicate the existence of genetic variation that is often as large as the variation in milk yield (Tables 6 to 8). Abdallah and McDaniel (2000) investigated genetic change in days open in North Carolina experimental dairy herd using an animal model and reported estimates of genetic, permanent environmental, environmental, and phenotypic variances of 155, 229, 5,081, and 5,465 $days^2$, which were larger than the median estimates of 103, 114, 2,284, and 2,500 $days^2$, respectively, in the present study. However, the mean of days open in their study was 143 days resulting in similar coefficient of additive genetic variation of 9%.

Because of large environmental variation, the median heritability estimate for days open was small (0.04, Table 19). However, Makuza and McDaniel (1996) also

Table 19. Estimated variance components[1], heritability (h^2), repeatability (r), additive genetic coefficient of variation (ACV%), and standard error (SE) for reproductive traits[2], and genetic, environmental, and phenotypic correlations for milk yield with reproductive traits from across-parity analyses in Saudi Arabia.

	Variances				Parameters			Correlations[3] with Yield		
Trait	A	PE	E	P	h^2	r	ACV%	G	E	P
DO										
Min[4]	68	63	2145	2359	0.03	0.073	8	0.03	0.00	0.001
Max	186	153	2358	2617	0.07	0.1	13	0.78	0.27	0.31
Med	103	114	2284	2500	0.041	0.09	9	0.44	0.21	0.24
Mean	107	112	2278	2497	0.043	0.09	10	0.42	0.21	0.22
SE	2	1.6	3.6	4.3	0.0006	0.0004	0.0009	0.013	0.005	0.005
GL										
Min	0.25	0.05	1.0	1.3	0.14	0.22	0.5	-0.17	-0.1	-0.15
Max	7.8	2.15	30	39	0.22	0.26	2.64	0.10	0.2	0.17
Med	3.7	.91	15.8	20.16	0.20	0.23	1.81	-0.05	-0.03	-0.07
Mean	4.2	1.0	16.6	21.80	0.19	0.23	1.84	-0.06	0.02	-0.01
SE	0.17	0.05	0.64	0.85	0.002	0.0008	0.004	0.006	0.01	0.009
CI										
Min	60	60	2100	2287	0.025	0.07	7	0.17	0.18	0.19
Max	171	208	2480	2781	0.063	0.11	12	0.73	0.28	0.31
Med	112	111	2293	2591	0.048	0.09	10	0.51	0.24	0.26
Mean	118	113	2314	2546	0.045	0.09	10	0.44	0.24	0.26
SE	2	2	7	8.5	0.0007	0.0006	0.0009	0.01	0.002	0.002
AFC[5]										
Min	1.3	----	0.74	2.1	0.57	-------	4.4	-0.27	-0.16	-.15
Max	2.7	----	1.64	4.31	0.70	-------	6.4	0.22	0.26	20
Med	1.7	----	1.02	2.73	0.62	-------	5.1	-0.08	0.08	0.07
Mean	1.7	----	1.02	2.73	0.63	-------	5.1	-0.06	0.07	0.012
SE	0.008	----	0.005	0.012	0.001	-------	0.0001	0.0003	0.0003	0.003
NS										
Min	0.14	0	1.4	1.55	0.09	0.09	20	-0.16	-0.18	-0.16
Max	0.18	0	1.5	1.70	0.11	0.11	23	0.29	0.20	0.22
Med	0.16	0	1.46	1.63	0.1	0.1	21	0.19	0.12	0.15
Mean	0.16	0	1.47	1.63	0.1	0.1	21	0.19	0.10	0.13
SE	0.006	0	0.002	0.002	0.000	0.000	0.04	0.01	0.03	0.01

[1]A=Additive variance, PE=Permanent environment variance, E=Environmental variance, and P=Phenotypic variance.

[2]DO=days open, GL=gestation length, CI=calving interval, AFC=age at first calving, and NS=number of services per conception.

[3]G=genetic, E=environment, and P=phenotypic.

[4]Min=minimum, Max=maximum, and Med=median.

[5]Results for age at first calving were from analysis of first lactation only.

reported small estimates of .01 and .02 for current days open in second and third lactations for Holsteins from Zimbabwe. The estimate of permanent environment variance for days open was similar to the additive genetic variance resulting in a repeatability estimate almost double the heritability (Table 19).

Number of services per conception is the most genetically variable reproductive trait. The additive genetic coefficient of variation ranged from 20 to 23% and averaged 21% indicating that great variability exists within Holstein cows from Saudi Arabia for this trait. However, more environmental variation existed. The lower end of the range of estimates of heritability for number of services per conception (0.09, Table 19) calculated from 20 subsamples of Method R procedures was greater than what is reported in the literature utilizing different procedures and models. In the present study, the median of the estimated heritability for number of services per conception was .10 (Table 19) which is higher than typically reported, but not different from that of Faust et al. (1989). Permanent environmental variance for number of services was zero resulting in a repeatability estimate of the same magnitude as heritability .10 (Table 19). The low repeatability estimates for reproductive traits indicate that prediction of future reproductive performance will be difficult and inaccurate because of the weak relationship between animal performances in different lactations.

It can be seen from these estimates of variances, heritabilities, and repeatabilities for reproductive traits for Holstein cows performing under Saudi environmental conditions, that there is variability between animals as large here as in temperate areas and in some cases larger. Although most estimates of heritability for reproductive traits for Holsteins from Saudi Arabia are small, improvement by selection for reproductive

traits is possible. A low heritability may not mean less genetic variation, given a large phenotypic variance. We should not relay only on the magnitude of a heritability estimate because in artificially inseminated populations, such as dairy herds, large number of daughters can be attained; therefore, higher accuracy for estimated breeding values for a low heritable trait can be achieved. However, the must important fertility traits most be identified first.

Low repeatability estimates imply that little relation exists between reproductive performance in different parities of Holstein cows from Saudi Arabia. Thus, as in temperate areas, predicting the future reproductive performance of Holsteins from Saudi Arabia is difficult because the performance of those cows in one parity provides little knowledge about their performance in the coming parities.

Estimated phenotypic, genetic, and environmental correlations between milk yield and reproductive traits across parities are given in Table 19. Generally, phenotypic and environmental correlations between production and reproductive traits were positive (unfavorable). The highest unfavorable phenotypic correlations with milk production were for calving interval (0.26 and 0.26, median and mean, respectively) and, though small, the more favorable were for gestation length (-0.07 and -0.01, respectively). The median positive phenotypic correlations of 0.15, 0.24, 0.26, and 0.07 for milk yield with number of services per conception, days open, calving interval, and age at first calving respectively, imply that cows with high potential for milk production needed more services per conception, required longer time to conceive, had longer calving intervals, and were older at first parturition than low milking producers. Negative phenotypic relationships for production with gestation length, although small, imply that high

milkers had shorter gestation lengths than low milking cows (Table 19). Phenotypic estimates in this study are in agreement with reports by Dematawewa and Berger (1998) and Short et al. (1990) for Holsteins, Mantysaari and Van Vleck (1989) for Finnish Ayrshire, Harmas et al (1987) for Guernsey dairy cattle.

Genetic correlations between milk yield and reproductive traits were greater than phenotypic correlations in general (Table 19). Genetic relationship between milk yield and days open, calving interval, and number of services per conception were positive (antagonistic) and moderate in magnitude. These three reproductive traits are highly genetically correlated and for some they are part-whole related (i.e., days open and calving interval). Thus it not surprising that all three traits have similar relationship with milk yield. The interference of herd' management can inflates the genetic correlation between reproduction and production traits. It seems that dairy managers in Saudi Arabia are giving the high producers preferential treatment allowing them more opportunity to conceive. Because it is rationally for a well-managed herds that the probability of a high producing cow that is open to be culled is less than that of an open low producing cow. High producing cows, therefore, tend to have longer days open and calving intervals.

The median genetic correlation between milk yield and days open of 0.44 is smaller than the estimate of .72 by Kragelund et al. (1979) from an analysis restricted to 10 cows per sire from Israeli Friesians. Higher genetic correlations for days open with milk production were also found in the literature (Abdallah and McDaniel, 2000, Dematawewa and Berger,1998, and Hermas et al., 1987). However, Raheja et al. (1989) reported substantially smaller genetic correlation estimates between milk production and days open than the estimate in this study.

Relationships between milk yield with gestation length and age at first calving were negative (favorable) but small. With estimated genetic and phenotypic correlations of –0.05 and –0.07, respectively, milk yield and gestation length seem to be fairly independent genetically and phenotypically. The genetic correlation between milk yield and age at first calving (-0.07) indicate that daughters of high-yield sires inclined to mature at a younger age, hence enter the herd earlier. The environmental correlation between milk yield and age at first calving was positive (Table 19), causing the phenotypic correlation to be positive (Table 19). This negative genetic correlation estimate between milk yield and age at first calving indicates that higher producers have their first calve earlier than low producers. However, these relationships are small. Hence, selection for milk yield does not prolong gestation length nor reases age at first calving. A further implication of the low genetic correlation between milk yield and age at first calving is that adjustment of milk yield for this effect will not remove any genetic variation (Khan et al., 1999). Abubakar et al. (1986) and Lee (1975) found the genetic relationship between milk and age at first calving to be unfavorable, implying that genetically high milking cows had their first calves at an older ages than low milking cows. Our estimate of -0.08 for milk with age at first calving was substantially smaller than the estimate of -0.78 reported by Hermas et al. (1987). However, the range of estimates in the present study encompasses the estimate of –0.21 reported by Seykora and McDaniel (1983).

The genetic correlation between milk yield and calving interval of 0.51 was highly unfavorable. This means that selection for high genetic merit for milk production results in cows with longer calving intervals. However, most of the phenotypic variation

in days open and calving interval is from environmental origin (Table 19). The genetic correlation between calving interval and days open is known to be very high (i.e., 0.97, Silva et al., 1992). Hence, the genetic relation between milk yield and calving interval is almost completely attributed to days open because of the part-whole relationship between days open and calving interval. Rather higher genetic correlation estimates for the same traits have also been reported by Pryce et al. (2000) for Holstein cattle (0.61). However, our estimate is comparable to the estimate of 0.46 between 120-day milk and calving interval reported by Everett et al. (1966).

The genetic correlation between number of services per conception and milk production was moderate (0.19). Faust et al. (1989) reported a higher antagonistic relationship (0.445) between fat-corrected milk and number of services per conception. Berger et al. (1981) estimated correlations between milk and number of services per conception in different lactations and reported a range from 0.62 for first lactation to 0.10 for third lactation. Our estimate is in contrast to the very small negative estimates reported by Raheja et al (198).

The positive genetic correlations between milk yield and some reproductive traits are indicators of loss of fertility because that implies that Holstein cows that have higher genetic potential for milk yield from Saudi Arabia tend to be genetically inferior for reproductive performance to lower milking cows. Although small, the negative genetic correlations between milk yield and age at first calving (-0.08) and gestation length (-.03) indicate that increased genetic potential for production in Holstein cows from Saudi Arabia results in younger age at first calving and shorter gestation length.

Relationships between Reproduction and Production in Different Parities

Tables 20 through 23 present parameters for variance components, heritability, and coefficient of additive genetic variation for days open, gestation length, calving interval, and number of services per conception in the first three lactations. Phenotypic and residual variances for days open decreased as parity increased. Phenotypic and residual variances for gestation length increased with advancing parities. Calving interval showed a slight increase in phenotypic and residual variances from first to second lactation and a slightly decrease from second to third lactation. Phenotypic and residual variances for number of services per conception were greater in later parities than first parity.

Except for number of services per conception, older cows exhibited greater genetic variation for reproductive traits than younger cows. Genetic variance for numberof services per conception substantially increased in second lactation over first and third lactations. It seems that cows in their first lactation were not under stress due to production; therefore, high producers conceive just as fast as low producers as indicated by the mean number of services per conception in the first lactation (1.42, Table 5) and the small favorable median genetic correlation (-0.02, Table 23). However, in the second parity, the stress from first lactation production was more pronounced for high producers and resulted in greater number of services for the second parity. So what can be seen as an increase in genetic variance may reflect management's desire to keep high producers even though they conceive late. This relationship may also suggests that number of services per conception may be determined by different set of additive genes in different lactations.

The coefficients of additive genetic variation for fertility traits in different parities followed a pattern similar to that of genetic variance and ranged from 0.7% for gestation

Table 20. Estimates of variance components, heritability (h^2), additive genetic coefficient of variation (ACV%), and standard error (SE) for days open in different parities, and genetic, environmental, and phenotypic correlations with milk yield in different parities in Saudi Arabia.

	Variance[1]			Parameters		Correlations[2] with Yield		
Parity	A	E	P	h^2	ACV%	G	E	P
First								
Minimum	43	2,389	2,469	0.02	6.2	-0.07	0.2	0.23
Maximum	251	2,680	2,796	0.09	15	0.7	0.4	0.33
Median	91	2,525	2,660	0.033	9	0.36	0.3	0.28
Mean	105	2,538	2,644	0.04	9.5	0.35	0.29	0.28
SE	2.4	4.4	4.5	0.0009	0.001	0.013	0.002	0.0002
Second								
Minimum	62	2,075	2,177	0.025	7.4	-0.11	0.07	0.09
Maximum	414	2,487	2,684	0.15	19	0.68	0.33	0.31
Median	100	2,347	2,492	0.043	9.5	0.18	0.25	0.22
Mean	127	2,338	2,465	0.05	10	0.24	0.24	0.23
SE	5.5	6.7	7.5	0.002	0.1	0.015	0.004	0.003
Third								
Minimum	4.62	1,671	2,130	0.002	2.06	0.28	0.001	0.18
Maximum	632	2,326	2,816	0.27	24.18	0.99	0.28	0.39
Median	322	2,051	2,366	0.14	17.25	0.77	0.17	0.26
Mean	342	2,084	2,427	0.14	17.0	0.70	0.17	0.27
SE	9.5	7.4	9.0	0.004	0.2	0.01	0.003	0.003

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.
[2]G=genetic, E=environmental, and P=phenotypic.

Table 21. Estimates of variance components, heritability (h^2), additive genetic coefficient of variation (ACV%), and standard error (SE) for gestation length in different parities, and genetic, environmental, and phenotypic correlations with milk yield in different parities in Saudi Arabia.

	Variance[1]			Parameters		Correlations[2] with Yield		
Parity	A	E	P	h^2	ACV%	G	E	P
First								
Minimum	0.85	2.38	3.23	0.09	0.3	-0.61	-0.52	-0.47
Maximum	13	25.5	38.7	0.42	1.3	0.37	0.42	0.41
Median	4.27	11.2	15.5	0.27	0.7	-0.23	0.085	-0.18
Mean	4.8	12.3	17.1	0.27	0.7	-0.21	-0.05	-0.10
SE	0.15	0.34	0.47	0.004	0.001	0.015	0.013	0.013
Second								
Minimum	.60	3.31	3.9	0.08	0.27	-0.74	-0.57	-0.53
Maximum	21.0	51.5	69.0	0.71	1.6	0.90	0.7	0.81
Median	4.0	23	29.5	0.16	0.7	0.16	0.12	0.12
Mean	6.0	24.6	30.5	0.19	0.7	.025	.06	0.06
SE	0.3	0.8	0.9	0.008	0.02	0.03	0.02	0.02
Third								
Minimum	2.5	16	23	0.06	0.5	-0.96	-0.99	-0.91
Maximum	57	72	126	0.91	2.7	0.57	0.71	0.63
Median	12.5	45	59	0.23	1.3	0.29	0.13	0.09
Mean	15.7	41.5	57.3	0.27	1.3	-0.31	0.14	0.07
SE	0.8	1.2	1.5	0.1	0.03	0.03	0.03	0.025

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.
[2]G=genetic, E=environmental, and P=phenotypic.

Table 22. Estimates of variance components, heritability (h^2), additive genetic coefficient of variation (ACV%), and standard error (SE) for calving interval in different parities, and genetic, environmental, and phenotypic correlations with milk yield in different parities in Saudi Arabia.

	Variance[1]			Parameters		Correlations[2] with Yield		
Parity	A	E	P	h^2	ACV%	G	E	P
First								
Minimum	47.6	2,052	2,114	0.02	1.7	0.023	0.14	0.15
Maximum	176	2,869	2,972	0.08	3.4	0.70	0.34	0.34
Median	103	2,358	2,408	0.035	2.6	0.40	0.28	0.26
Mean	94.4	2,387	2,481	0.04	2.4	0.34	0.27	0.25
SE	3.5	17	16.8	0.002	0.0005	0.01	0.004	0.004
Second								
Minimum	47	2,163	2,223	0.02	2	-0.11	0.16	0.17
Maximum	207	2,745	2,802	0.08	4	0.72	0.35	0.31
Median	91	2,417	2,492	0.04	2.5	0.38	0.26	0.25
Mean	105	2,401	2,506	0.04	2.5	0.36	0.25	0.25
SE	2.5	8	9	0.0009	0.00004	0.01	0.003	0.002
Third								
Minimum	89	1,559	1,775	0.04	2.5	0.28	0.06	0.11
Maximum	602	2,602	3,013	0.2	6.4	0.83	0.27	0.37
Median	279	2,213	2,418	0.12	4.3	0.74	0.19	0.27
Mean	315	2,165	2,480	0.12	4.5	0.66	0.16	0.26
SE	10	17	24	0.003	0.0007	0.01	0.004	0.004

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.
[2]G=genetic, E=environmental, and P=phenotypic.

Table 23. Estimates of variance components, heritability (h^2), additive genetic coefficient of variation (ACV%), and standard error (SE) for number of services per conception in different parities, and genetic, environmental, and phenotypic correlations with milk yield in different parities in Saudi Arabia.

	Variance[1]			Parameters		Correlations[2] with Yield		
Parity	A	E	P	h^2	ACV%	G	E	P
First								
Minimum	0.23	0.42	0.70	0.31	34	-0.21	-0.04	-.061
Maximum	0.33	0.54	0.83	0.44	44	0.17	0.1	0.075
Median	0.29	0.49	0.78	0.37	38	-0.02	0.044	0.024
Mean	0.29	0.49	0.78	0.36	38	-0.03	0.4	0.020
SE	0.002	0.002	0.002	0.002	0.1	0.004	0.002	0.002
Second								
Minimum	1.3	1.00	2.7	0.48	50	-0.01	-0.05	0.03
Maximum	2.02	1.45	3.1	0.66	63	0.28	0.15	0.16
Median	1.7	1.12	2.8	0.60	58	0.15	0.06	0.087
Mean	1.7	1.14	2.8	0.60	57	0.14	0.07	0.09
SE	0.012	.01	0.007	0.004	0.002	0.025	0.005	0.003
Third								
Minimum	0.06	1.6	2.10	0.03	11	-0.27	-0.02	0.07
Maximum	0.94	2.32	2.62	0.37	43	0.71	0.30	0.30
Median	0.31	1.95	2.33	0.13	24	0.31	0.12	0.16
Mean	0.36	2.0	2.33	0.15	25	0.32	0.12	0.16
SE	0.01	.01	.006	0.004	0.39	0.013	0.004	0.003

[1]A=Additive variance, E=Environmental variance, and P=Phenotypic variance.
[2]G=genetic, E=environmental, and P=phenotypic.

length in first and third lactations to 58% for number of services per conception in second parity. Considering the value of the coefficient of additive genetic variation in our study for all reproductive traits in each of the three first lactations (Tables 20-23), the traits ranked number of services first, followed by days open, calving interval, and gestation length. More variability implies more opportunity for improvement by selection; however, the heritabilities of these traits are small.

The median of heritability estimates for reproductive traits in the three lactations ranged from 0.035 to 0.60. The range of literature estimates for heritability for cow reproductive traits in different lactations is generally from 0.03 to 0.06 (Abdullah and McDaniel, 2000; Berger et al., 1981; Hermas et al., 1987; Raheja et al., 1989), although Dematawewa and Berger (1998) reported slightly higher estimates. Heritabilities for number of services and gestation length were larger than for calving interval and days open for the first two lactations. Days open, calving interval, and number of services exhibited similar heritabilities ranging from 0.12 to 0.14 in the third parity. The heritability for number of services per conception in the second lactation is extremely high. Except for the high heritabilities of number of inseminations per conception in first and second lactations, the heritability estimates for the reproductive measures in this study are comparable to those in the literature.

Presented in Tables 20 through 23 are phenotypic, environmental, and genetic correlations for milk yield and reproductive measures in each of the first three parities. Similar to the across parities estimate, phenotypic, environmental, and genetic correlations were moderate to high but were unfavorable in general. Reproductive measures showed higher genetic correlations than phenotypic correlations in all parities,

with some exceptions. Relative to lactation number, no distinct pattern was observed with the estimates of phenotypic and genetic correlations. High phenotypic and genetic correlations between yield and calving interval and days open support the previous evidence of the existence of antagonistic relationships between milk yield and fertility traits. Phenotypic correlations between milk and days open in all three parities are in agreement with those by Dematawewa and Berger (1998). These authors reported genetic correlations between yield and days open for first and second lactation that are higher than in our study; however, the estimate in the third parity in the present study is comparable to their estimate in the third lactation. But our estimates are substantially greater than those of Raheja et al. (1989). The correlation between milk and gestation length in the first lactation is a favorable, indicating selection for yield results in shorter gestation for first calving cows; however, a more antagonistic relationship is exhibited in the later parities.

It can be seen from the results presented in the foregoing chapters that high producing Holstein cows from Saudi Arabia exhibit variation for reproductive traits at least as great as that for cows in temperate areas and in some cases greater. Genetic variation in particular is the avenue of genetic improvement. However, it is well established that higher milking cows show genetic and phenotypic antagonism between production and reproduction measures and Holstein cows from Saudi Arabia are no exception. Furthermore, there are indications that this antagonism is genetically based as can be seen from the moderate genetic correlation between production and reproduction.

To try to prevent deterioration in reproductive performance as a result of selecting for milk, Hermas et al. (1987) suggested incorporating reproductive traits in sire

evaluation. However, the relationships between milk production and fertility traits are mathematically and biologically complex and many factors other than genetic factors can contribute to this relationship. Management circumstances can inflate this relation genetically and phenotypicaly. For example, because high milking cows return to estrus late as a result of a strong negative energy balance in early lactation, management which allows high producers to have better chance to conceive than lower producers can influence the genetic correlation between milk production and days open and calving interval. Another factor is stress. High milkers are under a tremendous amount of stress due to production, and if this is accompanied with a stressful external environment, health problems are more likely to occur, leading to reproductive disorders and indirectly affecting milk production. Several studies have shown a strong relationship between reproductive disorders and milk production (Martin et al., 1986, O'Bleness and Van Vleck, 1962, Simerl et al., 1992). Therefore, in the short term, improvement of fertility in Saudi Arabia can be achieved by improving management in the areas of health, feeding, recording of fertility data, and culling of cows with poor fertility performance. In the long run, however, with availability of records from sires selected and proved under Saudi conditions for milk yield, it is important to consider fertility traits in the breeding program.

CHAPTER 5

CONCLUSION

Results from this study indicate that high yielding breeds could perform well with respect to production and reproduction under arid environment conditions provided good management. However, these results also substantiate the presence of highly significant genotype by environment interactions for milk yield and age at first calving between Saudi Arabia and the United States. Estimate for genetic correlations reported here for Holstein milk yield (0.68 and 0.17, for first and all lactations, respectively) and for age at first calving (0.10) between Saudi Arabia and the United States, suggesting that sires with daughters in United States are significantly reranked for mature equivalent milk and age at first calving for daughters in Saudi Arabia. The two environments involved were widely divergent, thus genetic adaptability to local environmental conditions seems to be of paramount important for production and reproduction efficiency. There is evidence of enough genetic variation in milk yield under Saudi environment conditions. Therefore, it may be useful for herds in Saudi Arabia to participate in a national sire evaluation to predict the merit of those sires with daughters with high performance under a Saudi environment.

With respect to fertility traits, cows performing under Saudi environmental conditions showed a variability as great as in temperate areas and in some cases greater. Although most estimates of heritability and repeatability for reproductive traits for Holsteins from Saudi Arabia were small, improvement by selection for reproductive traits

is possible. However, genetic and phenotypic correlations between mature equivalent milk and fitness traits under a Saudi environment were generally positive (unfavorable). Hence, the incorporation of reproductive traits in sire indices may be questionable.

Implications of Results

Results from this study document the existence of substantial genotype by environment interaction for milk yield and age at first calving between the United States and Saudi Arabia as indicated by low genetic correlations. Ranks of sires based on the performance of their daughters in both countries change dramatically. This result confirms the necessity of evaluating sires within Saudi Arabia. There is enough genetic variation between animals in Saudi herds to select and improve production by selecting from within Saudi populations. The advantage of within-country sire evaluations would be that dairies would obtain sire proofs that reflect the actual differences achievable by those sires' daughters under a Saudi environment. There is an experimental center in Saudi Arabia in the Alkharge region that has started to select, test, and evaluate young sires born in Saudi Arabia under a Saudi environment. However, results from this center are not published yet. I recommend that large dairy farms in Saudi Arabia should take advantage of this center and participate in a national sire evaluation that would eventually provide more accurate ranking of sires than rankings based on tests done in more favorable environments.

Results from this study revealed high genetic variation and small to moderate heritability for reproductive traits. Though heritability is small, defining the most economically important reproductive trait is necessary so it can be incorporated in sire indexes to help prevent the deterioration of reproductive traits that could accompany sire selection for milk production. Because it is influenced by other reproductive traits (i.e., days open, number of services, and gestation length), calving interval may be the best measure to represent reproductive efficiency.

CHAPTER 6

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