GENETIC PARAMETERS OF CONCEPTION RATE AND HEAT EXPRESSION RATE

by

CHYONG-HUOY HUANG

(Under the Direction of Ignacy Misztal)

ABSTRACT

The objectives of this study were to estimate genetic parameters of heat expression rate (HE) indirectly with simulated data and investigate the genetic correlation between conception rate (CR) and HE with Holstein data from commercial herds. Three different measures for HE were derived based on days open (DO), which is approximately equal to voluntary waiting period + [21/(CR*HE)] – 21: HE1 = 21(number of services)/(DO + 21); HE2 = minimum of [21/service interval (SI)] or 1, where SI is the interval in days between two consecutive services; and HE3 = missing record for the first service record or, for other service records, 0 if SI >21 days or 1 if SI ≤21 days. In the simulation study, cows were assigned two correlated breeding values for CR and HE; the genetic correlation was allowed to vary from −0.9 to 0.9. Field data were milk yield and service records from 2000 through 2003, which were obtained from Dairy Records Management Systems in Raleigh, NC. Seven traits [DO, CR, HE1, HE2, HE3, days to first insemination (DFI), and CR at first service (FSC)] were analyzed by bivariate threshold-linear sire or animal models. The genetic correlation between CR and DO was estimated to be −0.99 regardless of the magnitude and sign of the assumed genetic correlation between CR and HE for simulation data as well as for field data. In the simulation study, correlations between CR and HE2 or HE3 from bivariate models agreed well with the assumed correlation between CR and HE. The estimated heritabilities for cow fertility traits from field data ranged from 1.4 to 5.9% which are comparable to literature estimates. The estimated genetic correlations between DO and HE2 and between DFI and FSC were −0.46 to −0.66 and 0.09 to −0.34, respectively. Based on estimates from field data and simulation data, the genetic correlation between CR and HE is moderately positive. In conclusion, the indirect HE measures paired with other fertility traits are moderately useful for estimation of the underlying genetic correlation between CR and HE.

INDEX WORDS: Conception rate, Heat expression rate, Fertility.

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CHAPTER 1

INTRODUCTION

Important factors that affect the overall performance of a dairy herd include milk production, reproductive performance, and health problems. Intensive selection was focused on milk production for a long time; meanwhile, fertility has deteriorated worldwide. As a result, interest in fertility issues has increased in the last decade (as evidenced by an abundance of scientific studies), and the dairy industry agenda has been dominated by fertility-related problems.

Reproductive performance is complex and greatly influenced by many factors, which include milk production, heat stress (seasons), management (voluntary waiting period, synchronization, and service protocols), nutrition, cow age, and genetic background as well as others. Moreover, reproductive performance has many components and a low heritability because of a lack of comprehensive trait definitions, inclusive records, and sophisticated methodologies. Those complexities and difficulties for genetic evaluation of fertility delayed the inclusion of reproduction in the definition of aggregate merit of dairy cattle until recently.

Reproductive performance includes three stages: gamete formation (ovulation), fertilization, and embryonic and fetal development and maintenance. Most studies concerned with genetic evaluation have focused on fertilization, which is measured by traits such as calving interval, days open, pregnancy rate, conception rate, non-return rate, and number of services per conception. For the other two stages of reproductive performance, however, there are indirect, unobserved, or unrecorded traits such as heat expression and embryonic mortality. In this study, heat expression is used rather than heat detection because the variance of heat detection is relatively artificial.

Many studies of heat expression and embryonic mortality are the focus of physiology and endocrinology studies in small experimental herds. Without direct information on heat expression and embryonic mortality, routine evaluation of those traits with large data sets is impractical. To evaluate fertility comprehensively, it is necessary to understand and properly account for heat expression, embryonic mortality and interactions of multiple factors and other reproductive traits. The purpose of this study was to estimate the genetic parameters of heat expression rate without direct estrus detection records.

CHAPTER 2

LITERATURE REVIEW

Milk production has been an obvious target for genetic improvement because it was economically valuable to producers and could be changed fairly rapidly. According to USDA records (National Agriculture Statistics Service, 2007), the average milk production per cow increased from 2,412.6 kg in 1950 to 9,314.3 kg in 2007 (Figure 2.1). Meanwhile, fertility of dairy cattle has deteriorated worldwide (Lucy, 2001).

In the United States, the deterioration of reproductive performance has been of great concern for more than 20 years. New York cows revealed a drop in conception rate at first service (**FSC**) from 65% in 1951 to 40% in 1996 (Butler, 1998), and annual pregnancy rate (**PR**) of cows in Florida decreased from 22% in 1977 to 12% in 2002 (de Vries and Risco, 2005). Washburn et al. (2002) also reported a decline of 9% in heat expression rate (**HE**) (i.e. heat detection rate) and an increase of 43 days open (**DO**) from 1976 to 1999 in the Southeast. In Ohio, days to first insemination (**DFI**) increased by 4 days and extended DO increased by 15 days from 1992 to 1998 (Rajala-Schultz and Frazer, 2003).

The obvious decline in fertility has been reported not only in the United States but also in other countries. In the United Kingdom, conception rate (**CR**) had been reported at a 1% phenotypic decline per year from 1975 to 1998 (Pryce et al., 2000). López-Gatius (2003) observed a decline of PR in Spain from 42.3% in 1991 to 33.1% in 2000; at the same time, Olori et al. (2002) found a genetically increase of 0.14 days per year in calving interval (**CI**) between 1988 and 1998 in Ireland. Similarly, Ojango and Pollott (2001) reported an increase in CI of 0.9

days per year over 11 years from 1986 to 1997 in Kenya. For German Holstein bulls born between 1990 and 2001, DO EBV increased by 8.0 days (Liu et al., 2008). The strong deterioration of fertility during the last several decades could have been caused by several factors, such as intensive selection for high milk yield, less effort and accuracy in maintenance or improvement of fertility, and lack of complete reproduction records and sophisticated methodologies.

The dairy industry relies not only on high milk production but also on efficient reproduction to maximize profits. In the absence of efficient reproduction, the direct advantages of high genetic merit of milk production must be offset by the costs resulting from extra semen, embryonic loss, veterinary visits, involuntary culling, and heifer replacement (Britt, 1985; Ball and Peters, 2007; Olynk and Wolf, 2008). Efficient reproductive performance includes many components and stages that require both females and males to be functionally capable of successfully completing all essential stages. Therefore, males must produce and ejaculate normal fertile sperm, and females must produce and ovulate normal fertilizable oocytes. Additionally, females must provide a reproductive system compatible with estrus cycle reestablishment, sperm transport, capacitation, fertilization of oocytes, and embryonic and fetal development that finally result in a healthy birth.

Achieving an efficient CI is difficult because of the inherent complexity of fertility components. Dekkers et al. (1998) have shown that the persistency of milk production was 3.8 and 9.4% of economic value of 305-day yield for a CI of 12.4 and 13.0 months, respectively. Extending CI by up to 3 months had no significantly deleterious effect on profitability (Ball and Peters, 2007). In view of that, optimal reproductive performance could be reconciled with gradually improved milk production either through higher peak milk yield or greater lactation persistency.

FERTILITY FACTORS

Reproductive performance is affected by many factors. Long-term emphasis on genetic improvement of milk production has been identified as a primary factor. Heat stress (season) also has a strong influence on fertility decline. Lucy (2001) mentioned, however, that fertility was affected not only by milk production and heat stress (season) but also by cow age, postpartum diseases, calving ease, nutrition (energy balance), bovine somatotropin (**bST**) use, herd size, management (service protocols), voluntary waiting period (**VWP**), and inbreeding. Those effects might be intricately related and difficult to separate. For instance, VanRaden et al. (2004) reported that the antagonistic correlation of milk yield with fertility might be caused not only by poor heat expression and conception problems in high-producing cows but also by the owner's voluntarily waiting longer to begin inseminating those cows.

Milk production

Many studies have demonstrated that high milk production has an antagonistic relationship (genetic and phenotypic) with reproduction (Coleman et al., 1985; Van Arendonk et al., 1989; Cole et al., 1991; Nebel and McGilliard, 1993; Hoekstra et al., 1994; Hodel et al., 1995; Beam and Butler, 1998; Darwash et al., 1999; Royal et al., 2000; Veerkamp et al., 2001); however, some studies have also shown no correlations (Villa-Godoy et al., 1988; Raheja et al., 1989a) or even a positive correlation (Moate and Harris, 1983; Fulkerson, 1984; Buckley et al., 2003).

Those diverse findings reveal that milk production could be confounded with other factors; additionally, the effect of milk production could be measured not only in terms of milk yield but also protein yield, fat yield, fat-to-protein ratio, peak milk yield, and lactation persistency. Grieve et al. (1986) found that fat-to-protein ratio was negatively related to energy balance and that lactation persistency was expected to improve energy balance. Their study indicated that not only total milk yield but also fat, protein and their ratio should be considered when including milk production as an effect in fertility analyses. Milk protein yield, fat yield, and fat-to-protein ratio are often used as indicators of energy balance because milk protein concentration is influenced by the level of energy supply in cows (Coulon and Rémond, 1991).

Later studies (Loeffler et al., 1999; de Vries and Veerkamp, 2000) demonstrated that fat-to-protein ratio and fat percentage were good predictors of fertility; a strong decrease in fat percentage had a negative effect on energy balance during early lactation. Patton et al. (2007) showed that fertility traits (DO and FSC) were positively associated with milk protein concentration but not milk yield or peak milk yield. Gábor et al. (2008) reported that both CR and PR had a significant negative correlation with protein and fat yields, a positive correlation with protein-to-fat ratio and yet no significant negative correlation between milk production and CR. They also indicated that milk protein concentration could predict the time to first insemination and be useful for discovering fertility problems. In a genetic trend analysis, Liu et al. (2008) reported moderately unfavorable genetic correlations (0.17 to 0.41) between EBV of several fertility traits and daughter milk deviations for fat and protein yields.

Productive performance for milk yield can also be represented by peak milk yield and lactation persistency. For cows producing the same total milk yield, those with a lower peak milk yield and greater lactation persistency might have less negative energy balance (**NEB**) and, therefore, suffer less reproductive failure than those with higher peak milk yield (Bar-Anan et al., 1985; Lean et al., 1989). Haile-Mariam et al. (2003a) found a genetic correlation between lactation persistency and CI that was close to zero and inferred that selection for lactation persistency might not impair fertility. Few studies examined phenotypic and genetic correlations of peak milk yield or lactation persistency with reproductive performance. For milk production, however, milk, fat, and protein yields can be different over lactation and parities. The antagonistic relationship between production and reproduction can be diverse for cows with the same total milk yield but different lactation persistency. That diversity can be an interesting issue for further study.

Heat stress (season)

Before being domesticated, cows likely were seasonal breeders mostly during summer so that calves would be born in spring when fresh pasture quantity was greatest and quality was the best. However, after domestication, cow fertility was better with fall rather than spring calving because fewer cows express estrus or conceive during hot summer months following spring calving compared with cold winter months following fall calving. Many studies (Thatcher, 1974; Fuquay, 1981; Gwazdauskas, 1985; Ray et al., 1992; Silva et al., 1992; Buxadera and Dempfle, 1997; Nardone et al., 1997; Hansen and Arechiga, 1999; Wolfenson et al., 2000; Hansen et al., 2001; Rutledge, 2001; Jordan, 2003) have shown that heat stress has a strong impact on reproductive efficiency. The most common index used as an indicator of heat stress is the temperature-humidity index (**THI**). For instance, Ingraham et al. (1976) reported that CR decreased from 66 to 35% when THI increased from 68 to 78. The THI is a clear measure of heat stress and indicates when fertility is impacted most. Ravagnolo and Misztal (2002) used THI to determine that heat stress 2 days after insemination causes the greatest non-return rate (**NR**) deterioration.

Researchers found that cows that calved in fall and winter had the fewest DFI and DO (Silvia et al., 2002) and that their reproductive performance could remain high and unchanged over time during the following cool season (winter and spring) (López-Gatius, 2003; de Vries and Risco, 2005; de Vries et al., 2005; Huang et al., 2008). Moreover, seasons vary among regions in the United States. Oseni et al. (2003) found the highest mean and range of DO in the southeastern region compared with other regions. Depression of reproductive performance with seasonal calving is exacerbated by an insufficient time to recover from NEB during early lactation when recovery time for breeding overlaps peak lactation (Borman et al., 2004). On the other hand, poor reproductive performance also can be explained physiologically. Heat stress has been shown to prolong impaired ovarian function; a noticeable depression in oocyte quality was continuous until fall (Wilson et al., 1998a, b; Al-Katanani et al., 2002).

Along with global weather changes, the effect of heat stress (season) has progressively increased over the years. De Vries and Risco (2005) reported that since 1983 the decrease in annual PR was largest during fall (25 to 12%) and smallest during summer (12 to 6%). In our previous study (Huang et al., 2009), the CR of cows in southeastern states was 54% in June in the late 1980s and 51% in May in the late 1990s, which reflects the earlier start of heat stress during the late 1990s. These studies indicate that the relative impact of heat stress (season) on fertility has been intensified over time.

Nutrition

Not every feeding regimen can easily meet lactating cows' metabolic requirements. In spring, plenty of high quality and relatively cheap fresh pasture (fodder) is available. However, forages tend to be low quality, higher priced, and of limited quantity in late summer. The depression of reproductive performance for cows on a pasture system has been associated with extreme weight losses in early lactation when cows transform their body adipose tissue into energy needed to attain high milk production (Fulkerson et al., 2001). Some examples and evidence (Kolver and Muller, 1998; Buckley et al., 2000; Kennedy et al., 2003; Diskin et al., 2006) have been found that the total dry matter intake of cows is still inadequate to meet their energy requirements in a pasture system under the best conditions. That problem can be solved by maize-based total mixed rations, which are more likely to affect energy balance and fertility in early lactation.

Nutrient demand of the dairy cow increases dramatically as lactation approaches peak milk yield, and insufficient dietary intake typically results in a state of NEB (Butler et al., 1981). In addition, intensive genetic selection to improve milk production also has resulted in cows that have a genetic predisposition towards a worse NEB in early lactation. Canfield et al. (1990) showed that cows on a high protein diet (higher degree of NEB) had lower FSC than did those on a low protein diet (31 versus 48%). Physiologically, researchers (Elrod and Butler, 1993; Butler, 1998) concluded that diets with a high protein content diminished reproductive efficiency because excess degradable protein increased plasma urea nitrogen levels and had a detrimental influence on embryonic development during the luteal phase.

Energy balance during early lactation is the primary factor associated with fertility (Patton et al., 2007), but it is not easily measured. As an alternative, change in body condition score (**BCS**) is used as an indicator during early lactation because it is associated with fat mobilization (Komaragiri et al., 1998). Correlated response to selection for high yield leads to greater loss of body condition in early lactation and consequently more intense NEB (Pryce et al., 2001). Patton et al. (2007) found a favorable correlation between BCS and FSC; cows with high BCS (≥3.25) had higher FSC than did cows with low BCS (≤2.25). Oikonomou et al. (2008) also reported a genetic relationship between BCS and fertility traits; they found that BCS had a moderately favorable (0.22 to 0.28) genetic relationship with fertility.

Age and parity

Age and parity are other factors that influence fertility efficiency. Some studies (Matsoukas, 1975; Hillers et al., 1984; Buxadera and Dempfle, 1997; Kuhn et al., 2006) indicate that fertility efficiency declines as breeding age increases. More DO were associated with later parities (Stevenson et al., 1983; Marti and Funk, 1994). Eicker et al. (1996) showed an 8% decline in CR for the first parity compared with later parities. Liu et al. (2008) reported 12.7 additional days in the interval from first to successful insemination (**IFS**) between heifers and cows in their sixth lactation. Buxadera and Dempfle (1997) found a high genetic correlation between heifer and cow NS and concluded that the same genetic basis does exist for certain fertility traits measured in different stages of the reproductive life of cows. However, other researchers (Raheja et al., 1989c; Weller and Ron, 1992) reported almost no genetic correlation between heifer and cow fertility, which indicates that the heifer and cow fertility are genetically independent.

Management

Influential management factors include VWP to first insemination, service protocols (hormone synchronization, timed AI), and a deliberately longer service interval (**SI**). To avoid poor NEB during early lactation, a longer VWP, especially for high-producing cows, could improve reproductive efficiency (Grimard et al., 2006; Gábor et al., 2008). Clay and McDaniel (2001) showed that a cow bred before 50 days in milk (**DIM**) had a 5.5% greater chance of being rebred than a cow bred after 70 DIM; also, a cow bred after 139 DIM had a 3.3% lower probability of rebreeding than a cow bred at 70 to 79 DIM. Gábor et al. (2008) reported that PR was <20% for cows bred before 60 DIM compared with a PR >40% for cows bred after 60 DIM. A similar result was found for CR, which increased significantly from 15% at 50 DIM to 49% at 150 DIM (Huang et al., 2008). The other voluntary delay is prolonged SI, but no studies have been conducted on it because of a lack of direct records and easy confounding with silent heat, missed heat, and false heat detection.

In the past, the most significant and convenient enhancements to fertility efficiency without voluntarily extending CI utilized service protocols that included regulating hormones of estrous synchronization and timed AI, improving heat detection methods and effectiveness, and strengthening the skill and experience of AI technicians. According to a survey from Hoard's Dairyman Research Department, approximately 10% of US dairy herds use timed AI for breeding (Lucy, 2001). Caraviello et al. (2006) conducted a survey of 103 large US dairy herds for which mean herd size was 613 cows, and 87% of those herds used hormonal synchronization or timed AI. A timed AI protocol coupled with ovulation synchronization can yield a higher PR than normal AI without hormone treatment (Tenhagen et al., 2004). However, PR is dependent on the different synchronization methods (Navanukraw et al., 2004; Peeler et al., 2004). Pegorer et al. (2007) found no difference in PR when comparing two fixed-time protocols (Ovsynch/P4 and Presynch/P4), which agreed with other similar studies (Cartmill et al., 2001a, b; Chebel et al., 2004). On the other hand, some researchers (Alnimer et al., 2002; De Rensis et al., 2003; Cerri et al., 2004; Santos et al., 2004) found that some protocols could facilitate reproductive performance. Cerri et al. (2004) concluded that administration of 1 mg of estradiol cypionate with presynchronization could induce estrus and improve reproductive performance. In addition, Dalton et al. (2004) reported that CR could be greatly improved by using professional AI technicians (45%) rather than herdsman inseminators (27%).

Genetic background

Some researchers believe that genetic background is responsible for the depression of reproductive performance (Pryce and Veerkamp, 2001). In many countries, reduced fertility has been attributed to a higher proportion of genes from North America Holsteins (Butler, 1998; Buckley et al., 2003; Dillon et al., 2003). A New Zealand study (Lopez-Villalobos et al., 2000) reported that purebred Holstein cows under seasonal calving had a higher significant replacement rate because of poor fertility than did Holstein-Jersey crossbreds. Australian studies (White, 2001; Auldist et al., 2007) confirmed that Holstein-Jersey crossbreds had higher CR and PR than did purebred Holsteins but no significant difference in BCS. However, a Netherlands' study (Veerkamp et al., 2001) stated a higher percentage of Holstein genetics was associated with lower BCS, higher milk yield, and poorer fertility. Pegorer et al. (2007) showed that Gyr (Zebu) service sires had 5% higher CR than did Holstein service sires during summer.

Inbreeding could be another genetic effect with only a slight influence on reproductive performance. Hermas et al. (1987) reported that every 1% increase in inbreeding coefficient led to 0.17 more services, 2 more DO, and 3.3% lower CR. Wall et al. (2005) also had similar results with an inbreeding coefficient increase of 10% leading to 2.8 days longer CI, 1.7 more DFI, and 0.03 more services. Inbreeding coefficients should be considered not only for cows but also for service sires and the resulting calf (Kuhn et al., 2006).

Other factors

Many other factors could depress reproductive performance, but they are difficult to detect because of a lack of comprehensive information and methodology. A cow's health has a large effect on her reproductive performance as mammary and uterine infections increase the risk of infertility (Kaneene and Miller, 1994; Emanuelson and Oltenacu, 1998; Loeffler et al., 1999; Risco et al., 1999). Eicker et al. (1996) also showed that disease is a significant risk factor for CR; retained placenta, metritis, and cystic ovary decreased CR by 14, 15, and 21%, respectively. Opsomer et al. (2000) discovered that cows with ketosis and depressed milk protein content were also 11 times more at risk of having inactive ovaries after calving. Kadarmideen et al. (2000) found moderately high genetic correlations between disease (milk fever and mastitis) and fertility traits.

The use of bST, which began in 1932, could temporarily increase milk yield. After numerous studies and improvements related to animal and human safety, bST has been approved for use in more than 25 countries. In the United States, commercial sale of bST began in February 1994, and its use has increased progressively on US dairy farms (Bauman et al., 1999). Because bST would temporarily increase milk production, which is detrimental for reproductive performance, its use could diminish reproductive efficiency indirectly. In early research (Cole et al., 1991) found that primiparous cows administered bST in early lactation had not only much lower CR but also higher heat expression error than did cows without bST. Similarly, Collier et al. (2001) conducted a large study and found recombinant bST caused a 16-day increase in DO for primiparous cows but had no effect on multiparous cows. On the other hand, some studies stated that appropriately utilizing bST did not affect the reproductive performance of dairy cows and could even have some advantages (Bauman et al., 1999). Luna-Dominguez et al. (2000) showed that using bST to increase milk production could actually reduce DFI and DO. Santos et al. (2004) reported similar results: when cows had the same HE, those that received bST had a higher CR (52.9%) compared with those without bST (CR of 45.6%).

FERTILITY TRAITS

Many essential components of reproductive performance can be used as measurement traits; e.g., time and ability to return to the ovulation cycle after calving, the phenomenon and detection of estrus, the farmer's decision to delay insemination, the ability to conceive and maintain pregnancy after insemination, and lastly the time and ability to continue the ovulation cycle and then correctly detect estrus if failure of conception or an early embryonic loss occurs. A reproductive success or failure at several of those points can be estimated quantitatively from a population viewpoint or, in some situations, from an individual viewpoint. Fertility traits can roughly be categorized into three classes: physiological characteristics, time intervals, and success or failure traits. However, defining a comprehensive fertility trait that covers all features of reproduction is extremely difficult. Most studies use DO, a single time-interval trait, to represent overall reproductive performance. Some studies have used other interval traits similar to DO to represent various reproductive stages, such as DFI, IFS, and CI. However, several other traits also can represent each reproductive performance component separately, such as days to first estrus (**DFE**), HE, CR, embryonic mortality, and SI. Moreover, some studies have used FSC, PR, NR at various specified days after calving, and NS.

The majority of traits used are considered to be performance measures of female fertility only, but a successful conception depends on both male and female fertility. In the past, several studies have reported a slight variance among service sires (Boichard and Manfredi, 1994; Weigel and Rekaya, 2000; Clay and McDaniel, 2001; Averill et al., 2004), which may indicate that service sire has an effect on conception outcome. Two studies on genetic evaluation of Holstein cows in Germany also had similar results in which service sire explained a negligible amount (<0.15%) of the total variance for NR (Konig et al., 2008; Liu et al., 2008).

Most genetic analyses of fertility have used either time-interval or success/failure traits rather than physiological characteristics because those traits are easier to collect, which leads to larger data sets. Time-interval traits are continuous with skewed distributions and have more appropriate, well developed models and approaches. Another advantage of interval traits is their higher heritability estimates; however, interval traits are greatly affected by management factors. The interval traits such as DO, CI, DFI, and IFS require information for each calving date and first and last service dates, which may not be available, or each service could be subjectively decided by farmers, such as longer VWP for high-producing cows. Other management factors that may be of importance, such as low heat detection efficiency, delayed breeding during hot season, and utilization of synchronization, are not available from Dairy Herd Improvement records.

From an economic viewpoint, the time between two successful calving events (CI) is an easily assessed and defined measure. However, relatively high percentages (30%) of cows do not have a subsequent record of a successful calving and are culled or removed from herd because of fertility or milking problems. In addition, collecting CI records requires waiting a longer time until the next calving event occurs. For that reason, CI studies have used records only from primiparous cows.

Literature estimates (Hoekstra et al., 1994; Buxadera and Dempfle, 1997; Pryce et al., 1997; Kadarmideen et al., 2000; Veerkamp et al., 2001; Haile-Mariam et al., 2003b) of heritability for CI range from 0.02 to 0.05. Genetic correlations between 305-day milk yield and CI range from 0.19 to 0.58; genetic correlations of CI with other fertility traits (DFI, FSC, and NR at 56 days postpartum) are moderate to high (0.73, 0.71 and -0.49, respectively).

Calving interval includes DO and gestation length. Once the last service date is known, CI could be replaced by DO because gestation length is almost constant unless abortion or dystocia problems occur. Researchers also have divided DO into two parts: DFI (if the first-service record is available) and IFS. The advantage of using any of those three traits rather than CI is a much shorter waiting time for collecting data. However, the censoring problem would become more serious without pregnancy confirmation, which requires extra cost for veterinarian visits or a longer time for obvious pregnancy or calving.

Days open has been the most frequently used trait in genetic evaluation of fertility. Heritability estimates range from 0.02 to 0.07, and genetic correlations with milk production range from 0.05 to 0.63 (Berger et al., 1981; Seykora and McDaniel, 1983; Raheja et al., 1989a, b, c; Van Arendonk et al., 1989; Hayes et al., 1992; Buxadera and Dempfle, 1997; Pryce et al., 1997; Dematawewa and Berger, 1998; Abdallah and McDaniel, 2000; Veerkamp et al., 2001; Haile-Mariam et al., 2003b; Oseni et al., 2004; Mitchell et al., 2005; Liu et al., 2008). Although DO is a widely utilized fertility trait, it is confounded with other types of reproductive performance and influenced by many factors, which include the ability of the cow to re-establish her regular ovarian cycle, the owner's subjective decision on when to breed in terms of VWP, the cow's heat expression and accurate HE, and the owner's other management policies such as synchronization protocol or avoidance of breeding in hot climate, CR, and embryonic mortality.

Many studies also have used DFI to represent fertility performance. During early lactation, DFI is strongly influenced by VWP, which may be arbitrarily decided based on milk production. As a result, heritability estimates for DFI have larger ranges (0.03 to 0.13) than for DO; unfavorable genetic correlations with milk production have a moderate range from 0.03 to 0.44 (Berger et al., 1981; Faust et al., 1989; Raheja et al., 1989a, b, c; Van Arendonk et al., 1989; Weller, 1989; Hayes et al., 1992; Hoekstra et al., 1994; Pryce et al., 1997; Kadarmideen et al., 2000; Weigel and Rekaya, 2000; Veerkamp et al., 2001; Haile-Mariam et al., 2003b; Mitchell et al., 2005; Liu et al., 2008).

The second part of DO, IFS, has been studied much less than other interval traits. The interval from first to last service is an interesting but intricate trait for revealing true reproductive efficiency of cows with the same interval but different NS. The heritability estimates for IFS are much lower than for DFI and range from 0.01 to 0.02. Unfavorable correlations with milk production range from 0.14 to 0.28 (Hoekstra et al., 1994; Konig et al., 2008; Liu et al., 2008).

The third type of fertility traits is success or failure traits, which could be measured on a population or individual basis depending on definition. For a population, success/failure traits are expressed as a ratio from a group of animals and are not suitable for individual genetic selection. Alternatively, success/failure traits measured individually are discontinuous, binary or categorical, which require more intricate analyses, especially for censored data. The binary nature of success/failure traits makes their genetic analysis difficult and complex. Although such traits are difficult to analyze and typically have lower heritability estimates, the data can be collected earlier. Examples of such traits are PR, CR, FSC, NR at 60, 90, or 150 DIM, and NS.

The Animal Improvement Programs Laboratory, Agricultural Research Service, USDA (Beltsville, MD) conducted the first national genetic evaluation for cow fertility in 2003 using DO and an assumed VWP to calculate PR of bull daughters (VanRaden et al., 2004). The formula for daughter PR is 21/(DO – VWP + 11); without VWP information, the linear formula is daughter PR = 0.25(233 – DO). This daughter PR measures how quickly the cow becomes pregnant again and represents the percentage of non-pregnant cows that become pregnant during each 21 day period. In the study of VanRaden et al. (2004), data were limited to 50 to 250 DO as verified by next existing calving record. Heritability estimates were close to 0.04 for both DO and PR, and the genetic correlation between DO and PR was 0.99. Every 1% increase in predicted transmitting ability for PR led to a decrease of 4 days in predicted transmitting ability for DO. Pregnancy rate could also be analyzed as a binary outcome within each 21-day cycle, but the evaluation of those multiple observations results in much lower heritability (VanRaden et al., 2004).

Other data sources from commercial herds include all insemination records, which can be used to evaluate bull and female fertility over DIM while milk production and environment change over time (Clay and McDaniel, 2001). The reproductive trait for each insemination record is represented in a binary outcome in terms of CR. During early years, CR was a fertility measure expressed as a ratio of successful conception to potential breeding; it was not evaluated genetically or used for genetic improvement (Spalding et al., 1975; Gwazdauskas et al., 1983). For CR of individual cows, the most representative definition is the binary outcome (success or failure) for each insemination record; then the sire or animal effect is used to calculate heritability of CR. Heritability estimates for CR range from 0.01 to 0.08 (Ron et al., 1984; Taylor et al., 1985; Weller and Ron, 1992; Kuhn et al., 2006). Heritability estimates for FSC are similar to those for CR and range from 0.01 to 0.05; however, FSC is antagonistically associated with milk production (–0.07 to –0.65) (Faust et al., 1989; Hoekstra et al., 1994; Pryce et al., 1997; Kadarmideen et al., 2000; Veerkamp et al., 2001; Mitchell et al., 2005; Kuhn et al., 2006).

Another measure of CR is the inverse of NS. Few studies have estimated the heritability of that measure of CR, and the estimates (0.018 to 0.035) are similar to those for previous CR measures (Weller, 1989; Buxadera and Dempfle, 1997). However, most studies used NS as a categorical trait rather than CR, with heritability estimates from 0.01 to 0.08. Number of services per conception is unfavorably associated with production traits, and genetic correlations range from 0.12 to 0.64 (Berger et al., 1981; Faust et al., 1989; Raheja et al., 1989a, b, c; Van Arendonk et al., 1989; Hayes et al., 1992; Hodel et al., 1995; Buxadera and Dempfle, 1997; Dematawewa and Berger, 1998; Kadarmideen et al., 2000; VanRaden et al., 2004).

A final fertility trait that could be expressed either for a population or an individual is NR based on successful inseminations at various days postpartum. Non-return rate has been used particularly for determining the relative fertility of bulls in AI service; however, it is easily biased because cows may be rebred to a different bull or may be sold (Lineweaver and Spessard, 1975). In early years, NR has been quantified as the ratio in number of conceived cows to number of total serviced cows within each herd (Thatcher and Wilcox, 1973). Genetic parameters on an individual animal basis can be estimated by expressing NR as a binary outcome. Heritability estimates for such an NR range from 0.01 to 0.04, and detrimental genetic correlations with milk production range from –0.26 to –0.56 (Van Arendonk et al., 1989;

Hoekstra et al., 1994; Hodel et al., 1995; Weigel and Rekaya, 2000; VanRaden et al., 2004; Konig et al., 2008; Liu et al., 2008).

Stages that can be clearly identified in a complete reproduction cycle are gamete formation (ovulation), fertilization, and embryonic development and maintenance, which are then followed by the birth of a normal healthy calf. Those stages are not easy to quantify as a probability of being a successful event. Fertilization is the stage that has been most intensively studied because it is relatively easy to observe. However, an understanding of the causes of success or failure in each stage is necessary to analyze reproduction comprehensively.

HEAT EXPRESSION

Before fertilization, the first stage of successful reproduction is establishing ovulation cycles and obviously expressing estrus. Gwazdauskas et al. (1983) found a significant effect on estrus activity for sire within genetic groups using a least-squares model, which indicates a potential genetic influence. Recently, Haile-Mariam et al. (2003b) stated that estrus expression after parturition is more heritable than conceiving to service, which was also supported by results of earlier studies on directly measured postpartum anoestrous interval (Darwash et al., 1997; Pryce et al., 1999; Veerkamp et al., 2000; Weigel and Rekaya, 2000). At this stage, two important and representative fertility traits that have been extensively studied physiologically and endocrinologically are DFE and HE. The interval until commencement of luteal activity could be an indicator of successful ovulation, which is defined as the interval from calving to the first day when ≥2 consecutive milk samples have a progesterone level of >3 ng/ml (Royal et al., 2000). Darwash et al. (1997) investigated the interval from calving to commencement of luteal activity by using progesterone concentration in milk samples as a measure of luteal activity; they found a mean interval of 25.6 days with a heritability of 0.28. The interval increased by 2.2% with each parity and was 1.21 times longer for spring calving compared with fall calving. Veerkamp et al. (2000) applied the same technique to measure the time of first luteal activity and estimated a heritability of 0.16 for DFE. Earliest first ovulation occurred 3 weeks after calving with increasing milk progesterone. The time required to resume ovulation could be influenced by the rate of increasing milk yield during early lactation (32.0 days for slow increases compared with 57.1 days for rapid increases) (Kawashima et al., 2007).

The most substantial problem regarding declining reproductive efficiency is poor HE as a consequence of missed heat, false heat detection, or silent heat. Poor HE caused an estimated annual loss of over $300 million to the US dairy industry (Senger, 1994). The importance of obvious expression and accurate detection of estrus has been demonstrated in many studies. Esslemont and Ellis (1974a) showed that the interval from calving to conception is dependent on both the HE and CR. Barr (1975a) calculated that the days lost because of missed heat were highly correlated (0.92) with longer DO. Poor HE could contribute to a longer CI and a higher culling rate because of failed conception (Bailie, 1982b). The increase of HE from 55 to 85% could decrease DO from 124.3 to 92.7 days (Heuwieser et al., 1997). Dairy cows inseminated at an observed spontaneous estrous have higher CR than cows inseminated with a timed AI program alone (Nebel and Jobst, 1998). Diskin et al. (2001) showed that increasing HE by 12 to 15% could increase CR by 10%. Jordan et al. (2002) conducted an experiment in which cows were assigned to two synchronization programs and found cows in estrus at insemination had significantly higher CR for both service protocols (45.8 and 35.4%) compared with cows not expressing estrous at insemination (19.2 and 27.7%). The results indicate that even synchronization protocols need to be combined with more accurate heat expression to produce higher CR.

No study has estimated genetic parameters for heat expression because no direct record of heat expression has been available for large commercial herds. The HE used in past studies was not observed individually, and genetic parameters for selection have not been estimated. Further studies need to find a way to estimate genetic parameters of HE without direct information from large commercial farms.

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EMBRYONIC AND FETAL MORTALITY

The final stage of a successful reproductive cycle after fertilization is embryonic and fetal development and maintenance until birth of a healthy calf. Embryonic and fetal mortality represents a major loss of income to dairymen. Kummerfeld et al. (1978) reported that embryonic mortality was estimated at 22.7% based on decline in NR between 28 and 75 days after insemination, and an overall embryonic and fetal mortality rate was estimated to be around 45% based on the difference between fertilization rate (90%) and mean calving rate (55%) (Sreenan and Diskin, 1986). Those studies reveal the problem of embryonic mortality that has existed since the 1970s and highlight the importance of heat expression. The gap between the two estimates of embryonic mortality shows that farmers fail to detect estrus following an insemination because they usually assume that the cow is pregnant and do not watch her for subsequent heat.

The problem of embryonic and fetal mortality accumulates over time. Diskin et al. (2006) summarized reproductive outcomes from several published studies and found that calving rate dropped from 55% in 1980 to 40% in 2006 because of early embryonic death (Figure 2.2).

Moreover, the intensity of embryonic and fetal mortality could be varied because the definitions and measures are different. Gábor et al. (2008) found that even moderate-producing Holstein-Friesian cows have late embryonic loss around 14 to 18.3%, which is calculated by the number of pregnant cows at 60 DIM divided by the number of cows conceiving from 30 to 36 DIM. Bech-Sábat et al. (2008) used plasma progesterone concentrations to confirm pregnancy from 60 to 90 days of gestation and found 12.6% early fetal loss. In general, pregnancy loss of lactating cows was estimated to range from 7 to 33% between 28 and 98 days of gestation (Smith and Stevenson, 1995; Inskeep, 2002; Silke et al., 2002; Nation et al., 2003). Because embryonic mortality, fetal loss, and abortion rate were increasing despite improvements and developments in knowledge and technology of fertility physiology, prenatal loss potentially becomes the most important impact on reproductive performance and profitability of milk production.

Gestation length can be divided into two intervals: embryonic period (1 to around 42 days after insemination) and fetal period (42 days after insemination to parturition) (Bech-Sábat et al., 2008). Day 24 of gestation generally can be defined as the demarcation between early and late embryonic death (or early fetal death) (Diskin et al., 2006). For early embryonic mortality, distinguishing between conception failure and early embryonic death is extremely difficult without pregnancy confirmation. Few studies have quantitative information on early embryonic loss. Ryan et al. (1993) used ultrasonography and nonsurgical embryo collection to find 44 to 76% embryos lost between 7 and 14 days after insemination. Sartori et al. (2002) used a standard nonsurgical uterine flushing technique to collect embryos and evaluate fertilization at 6 days after insemination; they found that 47 to 67% of embryos had poor to degenerate quality scores. For late embryonic and early fetal death, Silke et al. (2002) investigated the extent and pattern of embryonic and fetal loss from days 28 to 84 of gestation in laboratory experiment and found

47.5% of total embryonic loss occurred before 42 days of gestation. In another experiment with 520 heifers and cows, Romano et al. (2007) reported 10% embryonic death (30 to around 45 days of gestation) and 4.5% fetal death (45 to around 60 days of gestation). During the fetal period, the placenta attaches to the uterine wall to build a fetal-maternal connection for a viable and effective uterine environment favorable to the fetus. An inhospitable uterine environment, such as residual endometritis or an incomplete or damaged placenta, leads to an increased risk of fetal death between 30 and 60 days of gestation (Hanson et al., 2003). Furthermore, as placental attachment is complete, the transplacental transmission of blood to the fetus also can transmit infectious diseases from dam to fetus. The fetal immune system is not sufficiently developed to fight infectious diseases until 120 to 140 days of gestation, and the highest fetal mortality could be expected between 70 to 80 days and 140 days of gestation (Hanson et al., 2003).

Causative factors for embryonic and fetal mortality generally can be categorized as genetic, physiological, endocrine, or environmental. Mechanisms of those factors and how they are involved with decreased fertility have not yet been clearly distinguished. Similar to fertilization performance, the effects on embryonic and fetal mortality include milk production, heat stress, genetic background, cow age, and disease. Additional factors that are more specific to embryonic and fetal mortality are singleton or twins and an additional corpus luteum (López-Gatius et al., 2002; Romano et al., 2007). Physiologically, other possible factors are oocyte quality, follicle persistency, and the duration of pro-estrus and subsequent luteal phase as well as progesterone concentration.

Milk production has an unfavorable positive correlation with embryonic and fetal mortality, and its influence may be different during the summer. Pegorer et al. (2007) showed that cows with above mean milk production (>27 kg/day) had greater pregnancy loss (45.9%)

than did low-producing cows (15.7%). Bech-Sábat et al. (2008) stated that high milk production increases metabolic rate because of greater intake of dry matter, which reduces plasma concentrations of steroid hormones (such as progesterone) that have an obvious influence on fertility and gestation. However, some studies (López-Gatius et al., 2002; Starbuck et al., 2004; Gábor et al., 2008) found no significant negative correlation between milk production and retention of early pregnancy (30 to 42 days), which indicated that milk production may not have unfavorable effects on embryonic and fetal mortality.

Service sire is another factor of embryonic and fetal mortality, which again is very difficult to evaluate and few studies have found statistically significant results. López-Gatius et al. (2002) reported that cows bred to a single service sire have 3.4 times greater risk of pregnancy loss from 38 to around 90 days of gestation than did cows bred to multiple service sires. Starbuck et al. (2004) found that one of the four most frequently used service sires had a much lower pregnancy retention rate than the others. Pegorer et al. (2007) investigated the influence of service sire and reported that cows inseminated with Gyr semen have higher CR and lower embryonic and fetal loss compared with Holsteins.

Cow age has a significant influence on embryonic and fetal mortality. Sartori et al. (2002) conducted their experiment during summer in Wisconsin and concluded that age was a significant factor for embryonic quality of heifers and cows. They reported a higher proportion of high quality embryos recovered at 6 to 7 days after ovulation for heifers (72%) compared with lactating cows (33%). Romano et al. (2007) confirmed that cows have a higher embryonic and fetal mortality (16.4%) compared with heifers (8.8%). Starbuck et al. (2004) not only compared heifers and cows but also divided cows into two groups: young (2 to 4 years old) and older (≥5 years old). They reported that young cows had higher pregnancy retention rate (89.7%) than did older cows (81.1%).

Increased risk of embryonic and fetal mortality for twin pregnancies increase could be the result of insufficient uterine space for two calves. López-Gatius et al. (2002) reported that cows carrying twins (21.4%) had 3.1 times higher pregnancy loss than did cows carrying singletons (8.2%). More recently, Romano et al. (2007) also found that singletons and twins have a significant impact on embryonic and fetal mortality: cows carrying twins had a higher embryonic and fetal death rate (25.5%) than did cows carrying singletons (12.9%). However, twin pregnancy may be compounded with other factors. Improvement of milk production has been suggested as the most important cause for increased twinning rate (Kinsel et al., 1998; Fricke and Wiltbank, 1999). The reproductive hormone prostaglandin $F_{2\alpha}$, which is used for synchronizing estrus, significantly increases the risk of twin pregnancies (Kinsel et al., 1998; López-Gatius et al., 2002). Moreover, Romano et al. (2007) stated that heifers have a much lower chance of having twins (0.6%) than do cows (12.8%).

Progesterone concentration could be an appropriate indicator of pregnancy confirmation and retention (Franco et al., 1987). Progesterone is required for maternal support of conceptus survival and development. Studies have demonstrated that progesterone concentration is positively associated with pregnancy maintenance during gestation. Franco et al. (1987) showed that cows with lower milk progesterone concentrations (<0.5 ng/ml) between 21 and 24 days after insemination suffered higher pregnancy loss between 24 and 63 days of gestation. This result had been partly confirmed by López-Gatius et al. (2002), who stated that the corpus luteum may show depressed progesterone secretion during the late embryonic and early fetal period in cows suffering pregnancy loss. Likewise, Starbuck et al., (2004) reported pregnancy maintenance to 7 to 9 weeks of gestation was related to blood progesterone concentrations at 5 weeks of gestation. They found cows with low blood progesterone concentrations (0.4 to 3.76 ng/ml) had lower pregnancy retention (80%) than did cows with median or high blood progesterone concentrations (96%). Later, Gábor et al. (2008) concluded similarly that serum progesterone concentrations between 30 and 36 days after insemination are significantly correlated to embryonic loss. In addition, Bech-Sábat et al. (2008) found a significant interaction between season and additional corpora lutea: cows with no additional corpus luteum were almost 4 times more likely to have early fetal loss during the warm season than the cool season. Because the corpus luteum is the major source of progesterone in the cow during early gestation, pregnant cows with two corpora lutea or more may have higher plasma progesterone concentrations.

CONCLUSIONS

Most of the studies concerned with genetic evaluation of fertility have been primarily focused on fertilization, but complete reproductive performance includes three stages: gamete formation (ovulation), fertilization, and embryonic and fetal development and maintenance. Those studies of fertilization generally were concentrated on single traits, genetic correlations between observed traits, and the influence of single factors. For those indirect, unobserved, or unrecorded traits and the interactions of multiple factors and traits, few studies have been done because of a lack of appropriate information and methodology.

Deterioration of overall reproductive performance has been shown to be highly associated with superior genetic merit for milk production. The depression of reproductive performance leads to longer CI, higher involuntary culling rates, fewer calves per year, higher replacement costs, and lower profitability returns. Efficient milk production in either a pasture-or maize-based system requires a compromise between an appropriate CI and a low culling rate due to infertility. Achievement of those goals requires resumption of a regular ovulation cycle, efficient and accurate heat expression and detection, and high CR and pregnancy retention, especially for modern Holstein cows of high genetic merit.

Based on review of the literature, the following topics are of interest:

- Heat expression and detection without direct information. According to studies on reproductive performance with different HE using synchronization protocols, estrus expression and detection were different even under synchronization and resulted in different PR (Dalton et al., 2005; Walsh et al., 2007). Estrus expression and detection are important and vary individually even under synchronization.
- Interaction among heat stress, high milk production, and fertility. Heat stress strongly depresses both milk production and fertility, and high milk production also can impact reproductive performance. How much does heat stress affect the interaction between reproductive performance and milk production for high-yield cows?
- Different influences of genetic merit for high production on fertility. High milk production could result in a high peak milk yield or prolonged persistency, and fertility has been shown to be impacted by production during early lactation. Furthermore, some studies have found different correlations between production and reproduction. Is there any variability of reproductive performance among high-producing cows with low peak milk yield and high persistency?
- Interaction between environment and genetics of heat tolerance in dairy cattle as related to high production or reproductive performance.

- Estimation of genetic parameters of embryonic and fetal mortality without pregnancy confirmation.

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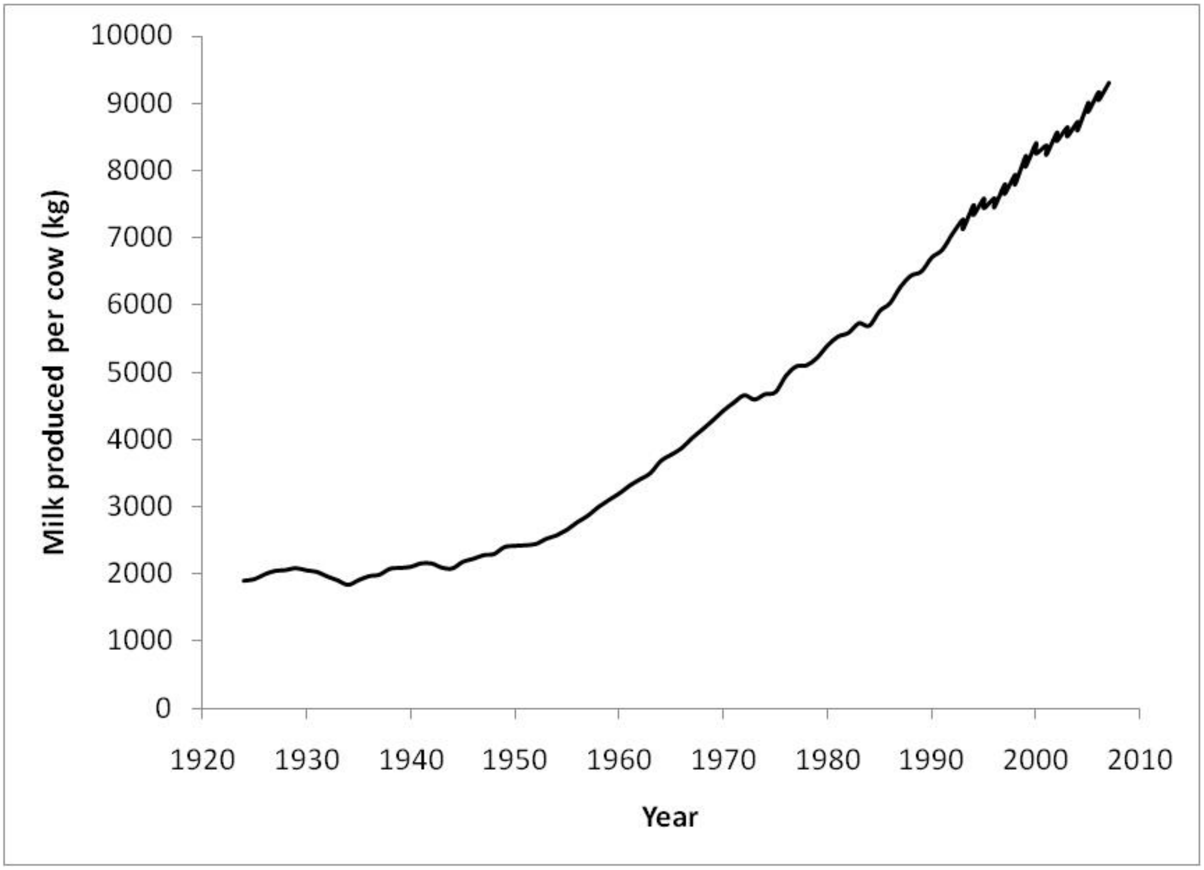

Figure 2.1. Mean milk yield produced per cow in the United States.

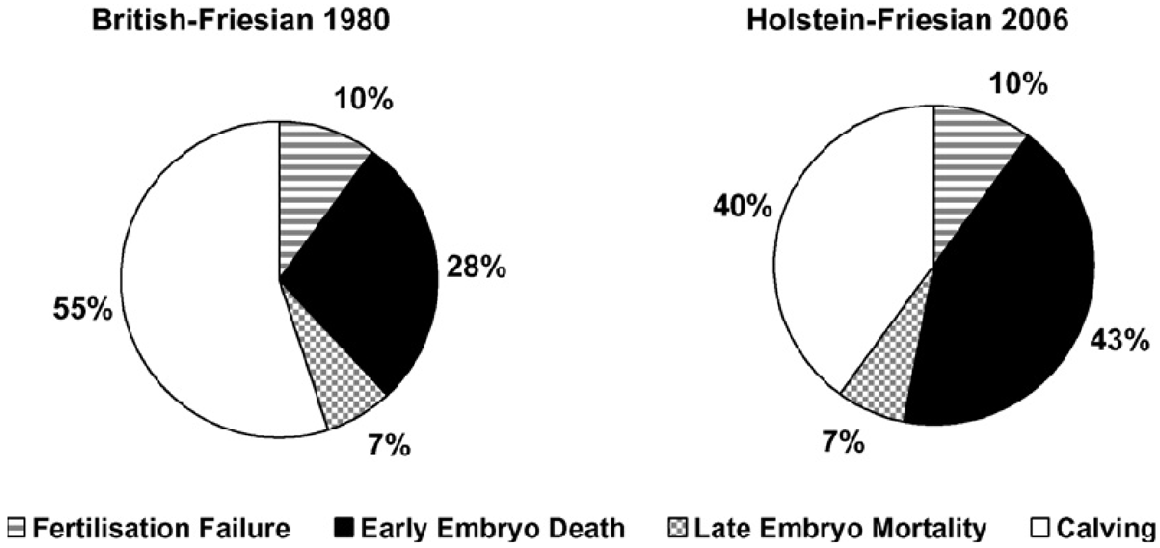

Figure 2.2. Reproductive outcomes for British-Friesian versus Holstein-Friesian cows.

From Diskin et al., 2006.

CHAPTER 3

STUDY ON GENETIC PARAMETERS OF CONCEPTION RATE AND HEAT EXPRESSION RATE

ABSTRACT

The purpose of this study was to estimate genetic parameters of heat expression rate (HE) indirectly. Days open (DO) is a composite trait with many components, including conception rate (CR) and HE. Three different HE measures were derived from the definition of DO, which is approximately equal to [voluntary waiting period (VWP) + 21/(CR*HE) – 21]: HE1 = 21(number of services)/(DO + 21); HE2 = minimum of [21/service interval (SI)] or 1; and HE3 = missing record for the first service record or, for other service records, 0 if SI >21 days or 1 if SI ≤21 days. Data were simulated starting with 5,000 animals for the base population and continuing under random mating for 10 generations to total 29,714 cows with 330 sires. Genetic correlations of −0.9, −0.5, 0.0, 0.5, and 0.9 between CR and HE were examined. Three record subsets were generated based on 1) a 30% probability of missing records, 2) censoring of records for cows that failed to conceive by 250 days in milk, or 3) a combination of the two conditions to approximate actual farm practices. Seven traits [DO, CR, HE1, HE2, HE3, days to first insemination (DFI), and CR at first service (FSC)] were paired and analyzed using a bivariate threshold-linear sire model with season and level of daily milk yield as fixed effects, sire as a random additive effect, and animal as a random permanent environmental effect. Genetic correlation between CR and DO was −0.99 for all data sets regardless of the magnitude and sign of the assumed genetic correlation between CR and HE. Genetic correlations of CR with HE2 or HE3 were similar and agree well with the assumed correlation between CR and HE. Because the genetic correlation between DO and CR was −0.99, genetic correlations between DO and HE2 or HE3 were opposite in sign as expected and similar for HE2 and HE3. Results for the paired traits DFI and FSC also agree well with the assumed correlation between CR and HE but could not account for the change of CR and HE with days in milk. The genetic correlation between CR and

DO is not a reliable indicator of the genetic correlation between CR and HE because DO depends on CR to a greater extent than CR does on HE. The estimated genetic correlation between CR or DO and HE2 or HE3 can reflect part of the true genetic correlation between CR and HE as well and may be useful for estimating that underlying correlation. The bivariate model with DFI and FSC has a certain advantage over the other traits as it allows early estimation of the genetic correlation between CR and DO dependence. Fertility traits are very complex, confounded with each other, strongly affected by data quality, and require more elaborate modeling than was done for this study.

Key words: Fertility, Conception rate, Heat expression rate.

INTRODUCTION

For a long time, selection in dairy herds focused on improvement of milk production (volume and composition) with little concern for reproduction. The deterioration of reproductive performance began becoming more noticeable 20 years ago (Philipsson, 1981; Jansen, 1985) and has since been reported worldwide (Butler, 1998; Pryce et al., 2000; Lucy, 2001; Ojango and Pollott, 2001; Washburn et al., 2002; López-Gatius, 2003; Rajala-Schultz and Frazer, 2003; de Vries and Risco, 2005). Although the initial reasons for leaving reproduction out of the selection process were predominantly economic, its complexity, low heritability, and lack of comprehensive trait definitions, records, and sophisticated methodologies postponed its inclusion in evaluations of overall merit for dairy cattle until recently.

Fertility is the main component of the reproduction complex. However, impregnation (0 or 1), the sole direct measure of fertility, is dependent on numerous factors. Physiologically, the ovulation cycle of a non-pregnant cow is approximately a 21-day interval, but the mean service interval (**SI**) from field data has been much longer possibly because of missed heat, false heat detection, silent heat, anestrous, conception failure, or a farmer's decision to skip insemination. Esslemont and Ellis (1974) showed that the interval between calving and conception is dependent on both heat expression rate (**HE**) (i.e. heat detection rate) and conception rate (**CR**). Barr (1975) reported a correlation of 0.92 between days open (**DO**) and delay due to missed heat, anestrous, and embryonic loss, which can be calculated as DO – voluntary waiting period (**VWP**) – (21/2) – [21(number of services per conception (**NS**) – 1)]. An increase of HE from 35 to 75% could decrease DO more than 25 days (Heuwieser et al., 1997). Moreover, low HE leads to a higher involuntary culling rate and longer calving interval (**CI)** because of conception failure (Bailie, 1982b).

The above studies clearly demonstrate the importance of heat expression in reproductive performances. Heersche and Nebel (1994) presented 8 methods to approximate heat expression efficiency as the percentage of possible estrus that were observed over a given time from herd summary information. In this study, HE is used rather than heat detection rate because the variance of detection is relatively artificial whereas expression variation is genetic. In reality, however, no direct heat expression/detection records have been collected in a database; thus, genetic parameters for HE, which are indispensable for eventual inclusion as a selection criterion, cannot be estimated directly.

Because the measurable trait DO is influenced by both HE and CR, which is measurable as well, investigating the relationships among those traits might provide an indication of genetic parameters for HE.

MATERIALS AND METHODS

Simulation

Animal Care and Use Committee approval was not obtained for this study because simulated data were used. The simulation steps are shown in Figure 3.1. The data were simulated starting with 5,000 individual animals for the base population and continuing under random mating for 10 generations to total 29,714 cows with 330 sires. Each animal was assigned two correlated breeding values for CR and HE. To clarify calculation, assumed heritabilities were as high as 0.15 for CR and 0.08 for HE. Genetic correlations of −0.9, −0.5, 0.0, 0.5, and 0.9 between CR and HE were examined. Each cow was assigned 1) a calving month generated from a uniform distribution, 2) daily milk yield generated from a normal distribution with a mean of 30 kg and a variance of 40 kg^2 and also restricted within 10 to 50 kg, 3) days of first estrus (**DFE**) generated from a normal distribution with a mean of 45 days and a variance of 50 days^2 and also restricted within 20 to 70 days, and 4) a VWP generated from a uniform distribution but dependent on daily milk yield. For cows with low daily yield (<24 kg, which is mean – 1 standard deviation), 50% did not have a VWP, and the other 50% had a VWP generated form a uniform distribution restricted from 50 to 70 days. For cows with moderate daily yield (24 to 36 kg), 30% had no VWP, and VWP for the remaining cows were distributed uniformly from 50 to 90 days. For cows with high daily yield (>36 kg), 90% had VWP that were distributed uniformly from 50 to 110 days. A regular estrus cycle was defined to last 21 days, and days in milk (**DIM**) at service was equal to DFE + 21(number of cycles); service month could be calculated from calving month and DIM at service.

The underlying liabilities of CR and HE were based on following sire model:

$$\mathbf{l} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e}$$

where **l** = vector of underlying liabilities of CR and HE; **b** = vector of fixed effects of service month and level of daily milk yield; **u** = vector of random sire effect as additive effect; **p** = vector of random cow effect as a permanent environmental effect; and **X**, **Z**, and **W** = incidence matrices for **b**, **u**, and **p**, respectively; and **e** = vector of random residual effects. Variances were defined as

$$\mathrm{var}\begin{bmatrix}\mathbf{u}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_{\mathrm{s}}^2 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\sigma_{\mathrm{pe}}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{\mathrm{e}}^2\end{bmatrix}$$

where σ_{s}^2 = sire variance as additive genetic variance; σ_{pe}^2 = animal variance as permanent environmental variance; σ_{e}^2 = residual variance; **A** = additive genetic relationship matrix for sire; and **I** = identity matrix for cows.

Means were 0.5 for HE and 0.4 for CR. Service record was 0 or 1 if the liability of HE was lower or higher, respectively, than the threshold point. The maximum DIM at service was set at 999 days, and cows that failed to conceive (<3% of the whole data set) were disregarded. Thus, the created data set contained records for cows that eventually conceived and was named ALL. The ALL data set was used to generate three subsets of data that approximated actual farm conditions more closely. To reflect the uncertainty of field data, the first data subset (MIS) consisted of records after allowing a 30% probability for each service record to be missing. If the last service record was designated as missing, the previous record was treated as the last one; similarly, if the first service record was missing, the next one was treated as the first one. To address censoring of fertility records on farms, the second data subset (CEN) included records censored at 250 DIM; i.e., observations on cows failing to conceive by 250 DIM were censored. The last data subset (CMS) combined the previous two conditions.

Definitions

The DO for each data record was decided by last service and calving dates, which could be approximately represented by the formula:

$$\mathrm{DO} \cong \mathrm{VWP} + \frac{21}{\mathrm{CR}*\mathrm{HE}} - 21, \tag{1}$$

where CR is the inverse of NS. Then equation 1 was transformed into an overall HE (**HE1**):

$$\mathrm{HE1} = \frac{21*\mathrm{NS}}{\mathrm{DO} - \mathrm{VWP} + 21} \text{ or} \tag{2}$$

$$\mathrm{HE1} = \frac{21*\mathrm{NS}}{\mathrm{DO} + 21}\,. \tag{3}$$

Because VWP records were not available, equation 3 was used for HE1.

Equation 3 was modified to provide HE for each service record (**HE2**) based on SI and an estrus cycle of 21 days:

$$\mathrm{HE2} = \begin{cases} \text{missing} & \text{first service} \\ \min\left(\frac{21}{\mathrm{SI}}, 1\right) & \text{later services} \end{cases} \tag{4}$$

The HE2 at first service can be biased if days to first insemination (**DFI**), which may include unknown VWP, rather than SI is used. Therefore, the HE2 at first service was treated as missing.

The third HE measure (**HE3**) was based on a binary outcome (as done for CR), but the success or failure of heat detection was determined as a function of SI.

$$\mathrm{HE3} = \begin{cases} \text{missing} & \text{first service} \\ 0 & \mathrm{SI} > 21 \\ 1 & \mathrm{SI} \le 21 \end{cases} \tag{5}$$

Same as HE2, HE3 at first service was treated as missing.

Seven traits [DO, CR, HE1, HE2, HE3, DFI, and CR at first service (**FSC**)] were analyzed with the following bivariate threshold-linear sire model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e}$$

where **y** = vector of binary outcomes for CR and HE based on the underlying liabilities, HE1, HE2, HE3, DFI, and FSC. Variance components were estimated with the programs GIBBS2F90 and THRGIBBS1F90 (Misztal et al., 2002) for continued and discrete traits, respectively. The programs are based on a Bayesian approach using Gibbs sampling for threshold and linear models. For each analysis, 20,000 Gibbs samples were discarded as burn-in, and every fifth sample from the following 15,000 samples was used to calculate posterior means and standard deviations for (co)variance component, correlation, and heritability estimates. Program restrictions required that first-service HE2 for the bivariate model for DO and HE2 be treated not as missing but the similar for other services (21/DFI or 1, whichever was smaller).

RESULTS AND DISCUSSION

Estimated genetic correlations between pairs of reproduction traits were plotted against assumed correlations between CR and HE (Figures 3.2 to 3.8). Those genetic correlations from the bivariate model were expected to be indicative of the known assumed genetic correlation between CR and HE. The original hypothesis that the genetic correlation between CR and DO might be an indicator of the genetic correlation between CR and HE because DO is a function of both CR and HE was not clearly supported. The genetic correlation between CR and DO remained highly negative at −0.99 regardless of the magnitude or sign of the assumed genetic correlation between CR and HE for all data sets (Figure 3.2). The negative correlations between CR and DO were particularly high and consistent for the CEN data set. For ALL and MIS data sets, the correlations between CR and DO weakened as the absolute value of the assumed correlation between CR and HE decreased. However, that tendency diminished as the data conditions became more complex, which indicated that the DO estimate was affected not only by

CR but also by quality of the raw data. Thus, genetic correlation between CR and DO cannot be a reliable indicator of the genetic correlation between CR and HE.

Changes in the correlation between CR and HE1, which was calculated from equation 3 because of the lack of VWP information, as the assumed correlation between CR and HE varied are shown in Figure 3.3. The relationship between the magnitudes of assumed and estimated correlations appeared almost linear. Nonetheless, the estimated correlations remained negative for the entire range of assumed correlations for the ALL, CEN, and CMS data sets. Only the MIS data set had positive correlations between CR and HE1 correlations when highly positive correlations between CR and HE were assumed. The absence of VWP information might be one reason for the differences between expected and estimated correlations for the ALL data set. However, the MIS data set had an unexpectedly great agreement between estimated and assumed correlations.

Estimated genetic correlations between CR with HE2 (Figure 3.4) were similar to those between CR and HE3 (Figure 3.5). For the ALL data set, genetic correlation of CR and HE2 was in almost perfect agreement with the assumed correlation between CR and HE. For the MIS and CEN data sets, estimated genetic correlation between CR and HE2 (or HE3) reflected part of the true genetic correlation between CR and HE as well. Correlations estimated for the CMS data set, which reflects farm conditions best, were much less consistent with assumed correlations between CR and HE, especially for HE3.

Estimated genetic correlations with DO are in Figure 3.6 for HE2 and Figure 3.7 for HE3. Because the genetic correlation between DO and CR was high and negative, the opposite genetic correlation was expected between CR and HE2 or HE3. Plots of the estimated correlations of DO with HE2 and HE3 with the assumed correlations for CR and HE were also expected to have similar slopes, with correlation magnitude as the main difference. However, as Figure 3.6 and Figure 3.7 show, the results were unexpectedly very different for HE2 and HE3. Estimated correlations between DO and HE2 for the MIS data set (Figure 3.6) and between DO and HE3 for the CEN data set (Figure 3.7) were unexpectedly close to assumed correlations between CR and HE, which indicates that the genetic correlation between DO and CR may not be −0.99, and that more sophisticated models are necessary for further study. This finding also reveals that DO should be adjusted based on other information such as VWP to remove bias. Finally, it seems that DO depends on CR more than CR depends on HE.

For DFI and FSC, the final pair of correlated traits, estimated correlations (Figure 3.8) for the ALL data set were very close in agreement with assumed values. Estimated correlations were only slightly higher for the CEN data set and somewhat lower for the MIS and CMS data sets. Nevertheless, all data sets appeared useful for the estimation of the underlying correlation between CR and HE. This bivariate model has a certain advantage over other traits as it allows early estimation of the genetic correlation between CR and HE. Bailie (1982a, b) demonstrated that DFI was significantly influenced by HE and VWP but not CR. Coleman et al. (1985) also stated that DFI is the major determinant of CI and depends more on HE than physiology. Huang et al. (2008) found that cows have different CR over time after calving; however, the change of CR and HE with DIM was not accounted for in the current study. Similar to CR, cows may have different HE over time, and the correlation between CR and HE may also change. Thus, more sophisticated models should be studied for DFI and FSC as well as for CR and HE2 or HE3.

In conclusion, fertility traits are very complex, confounded with each other, and strongly affected by data quality. Days open has a higher genetic correlation with CR than does HE but requires more elaborate definition and modeling than was done in the current study. In particular, VWP should be included in the definition of DO as well as HE measures. Nevertheless, estimation of the genetic correlation between CR and HE may be possible without direct HE observations.

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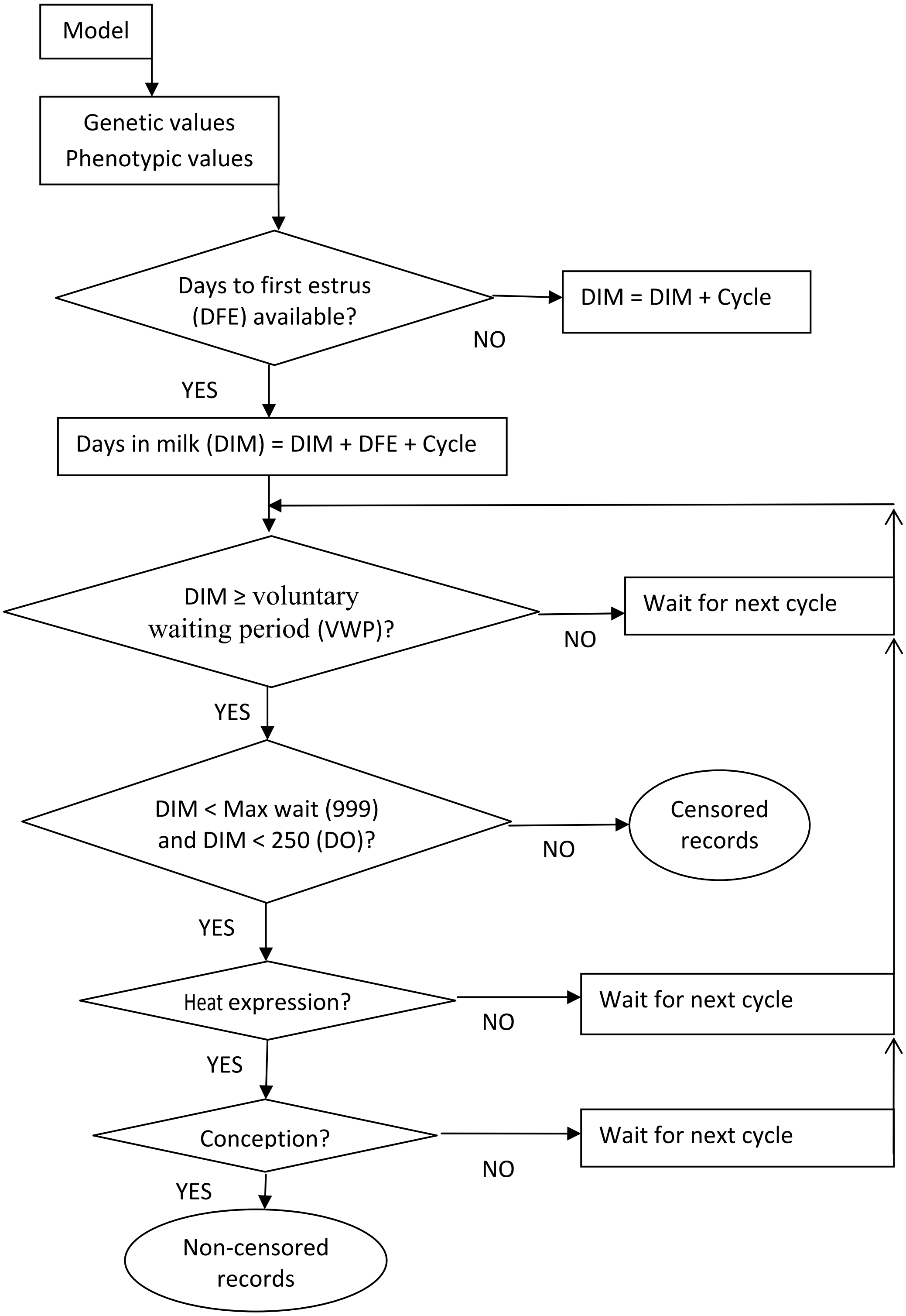

Figure 3.1. Process for data simulation.

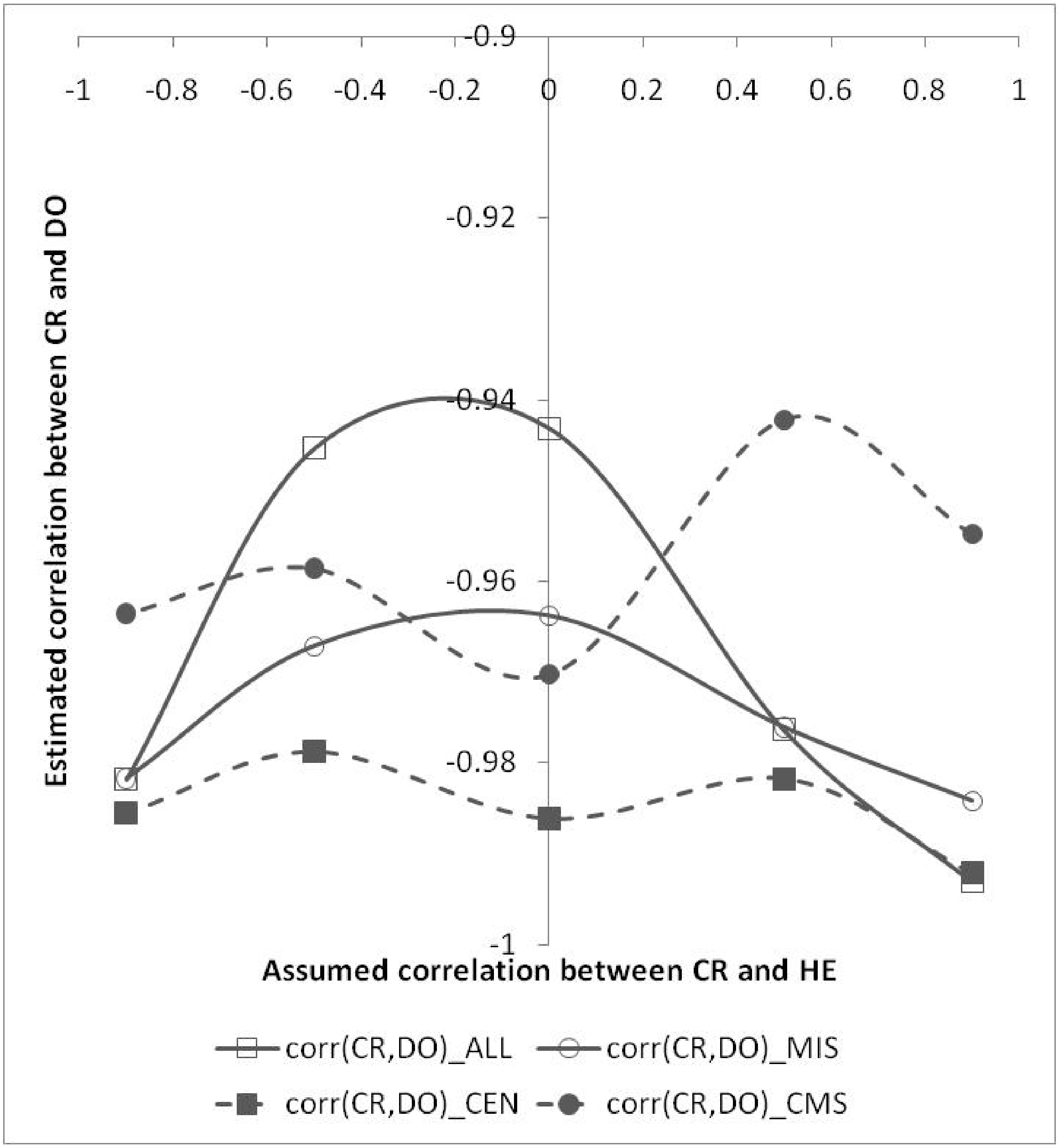

Figure 3.2 Estimated genetic correlations (corr) between conception rate (CR) and days open (DO).

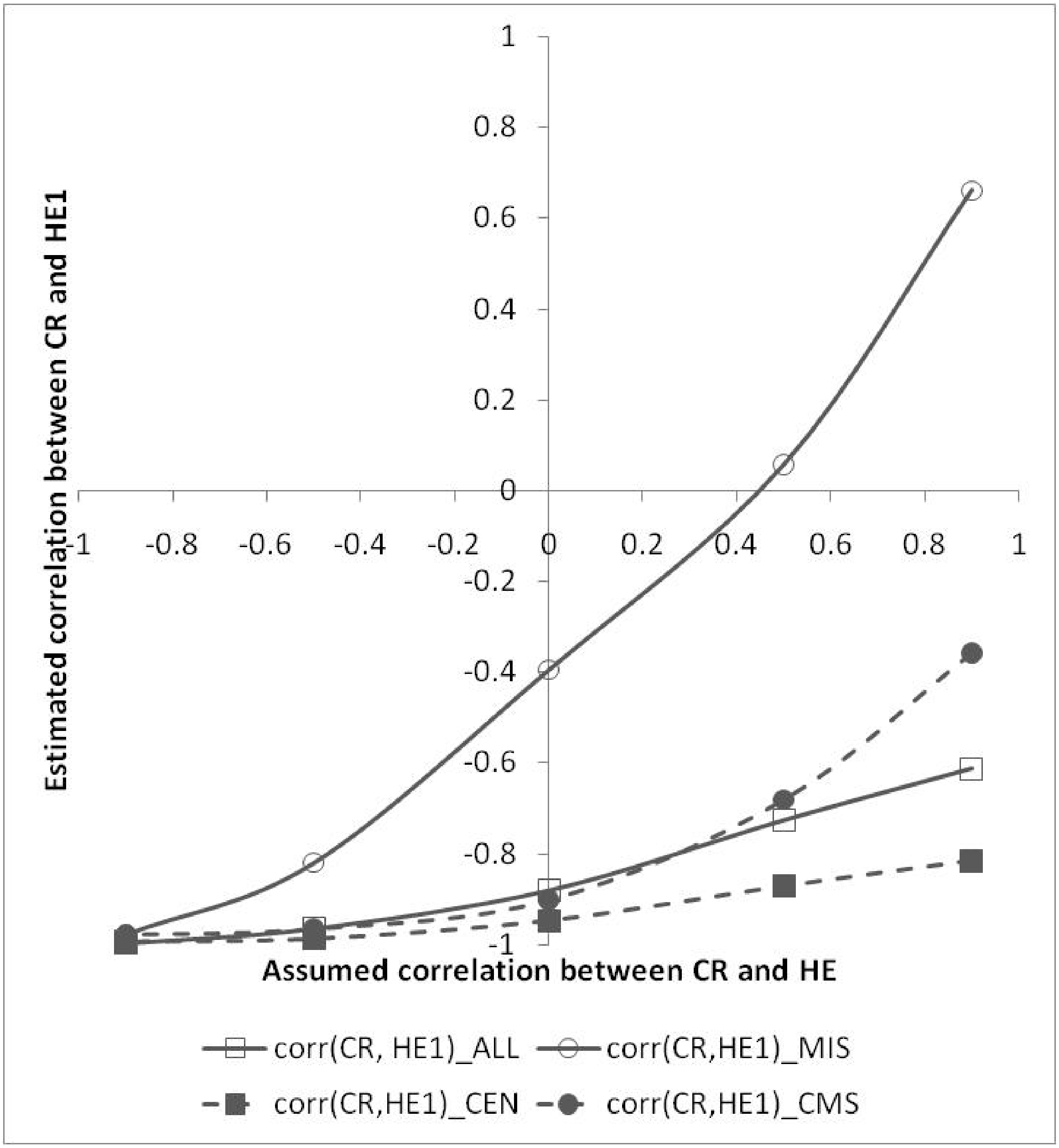

Figure 3.3. Estimated genetic correlations between conception rate (CR) and overall heat expression rate (HE1).

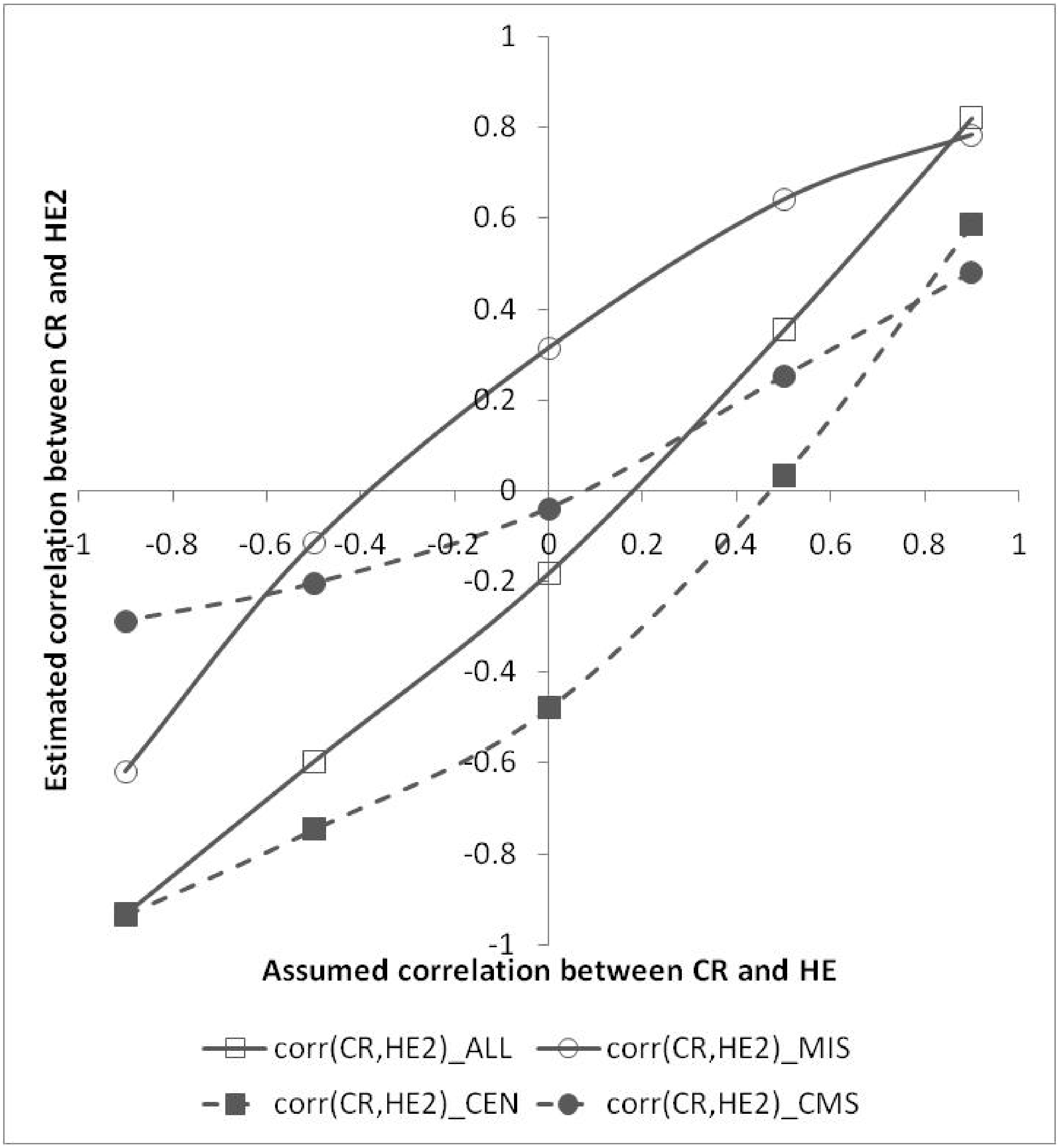

Figure 3.4. Estimated genetic correlations between conception rate (CR) and heat expression rate for each service record (HE2).

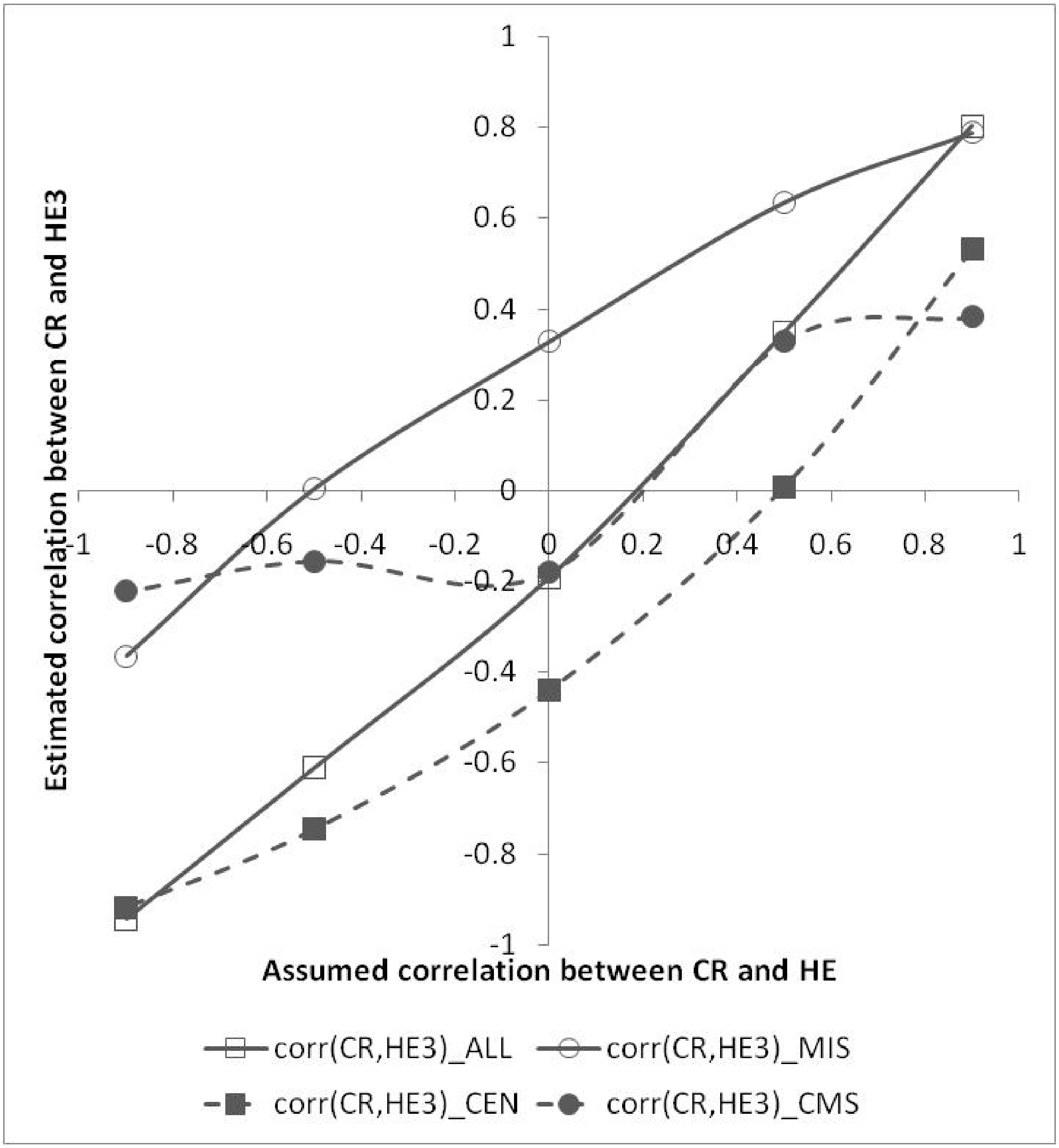

Figure 3.5. Estimated genetic correlations between conception rate (CR) and heat expression rate based on a binary outcome for each service record (HE3).

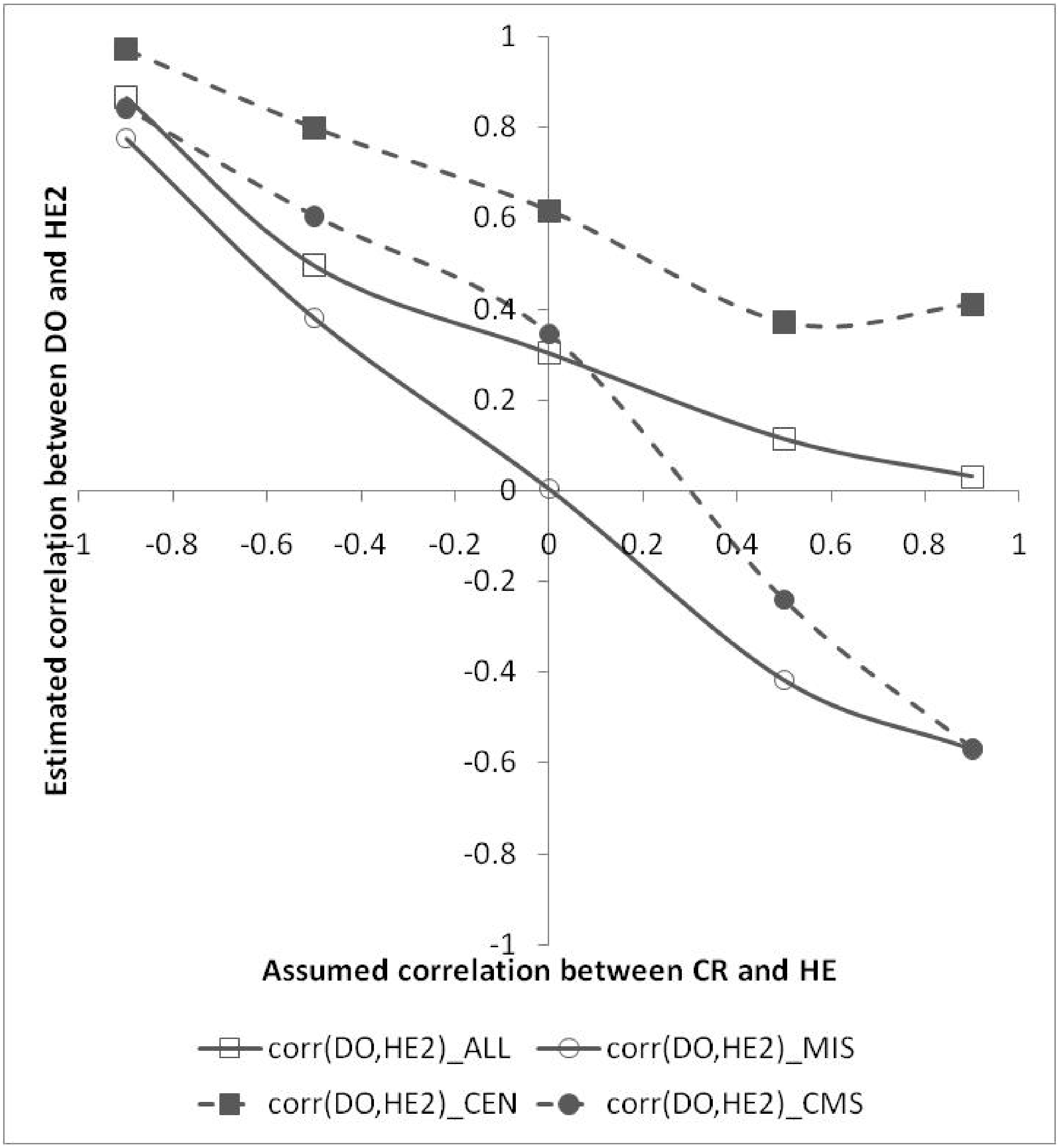

Figure 3.6. Estimated genetic correlations between days open (DO) and heat expression rate for each service record (HE2).

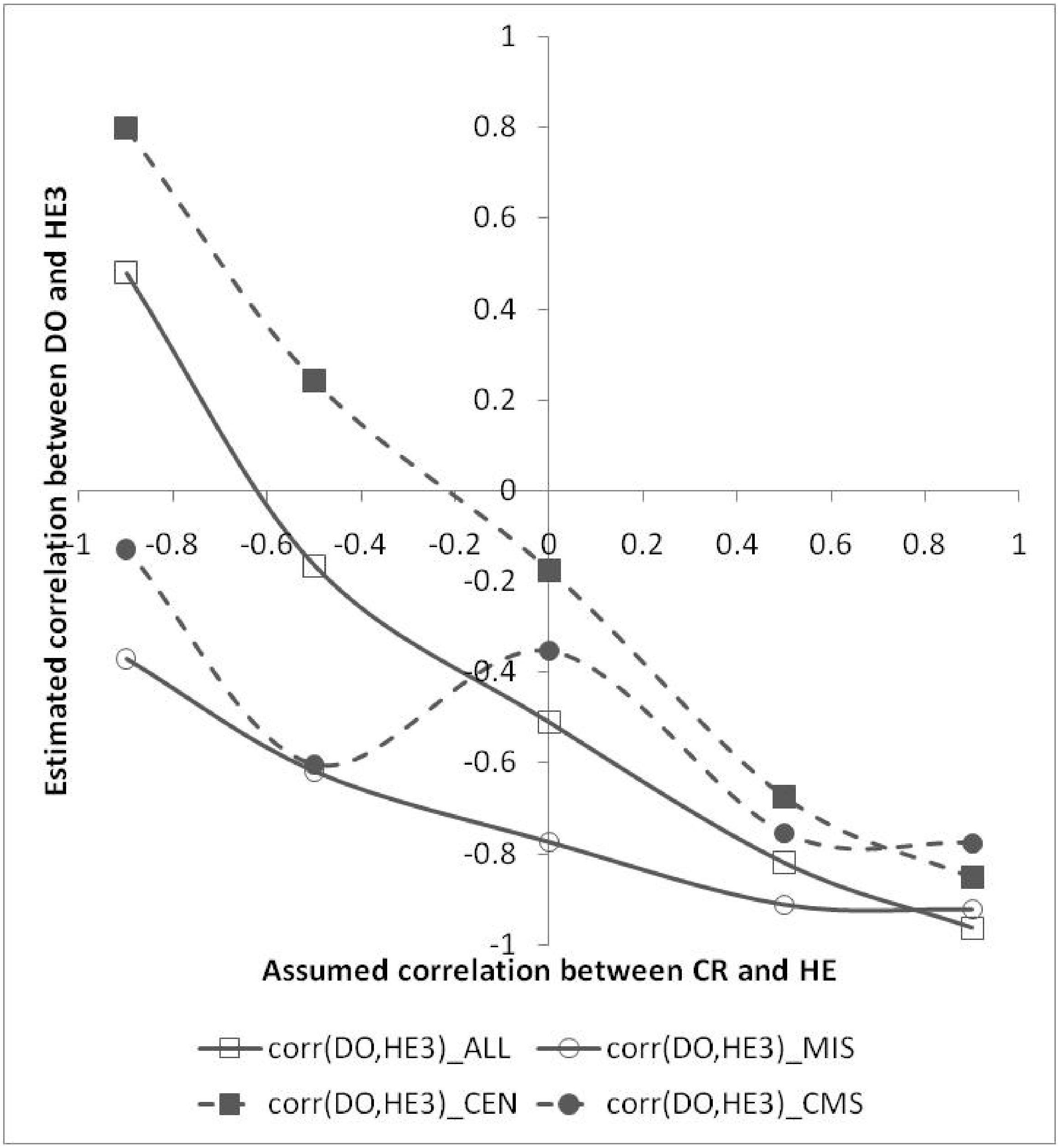

Figure 3.7. Estimated genetic correlations between days open (DO) and heat expression rate based on a binary outcome for each service record (HE3).

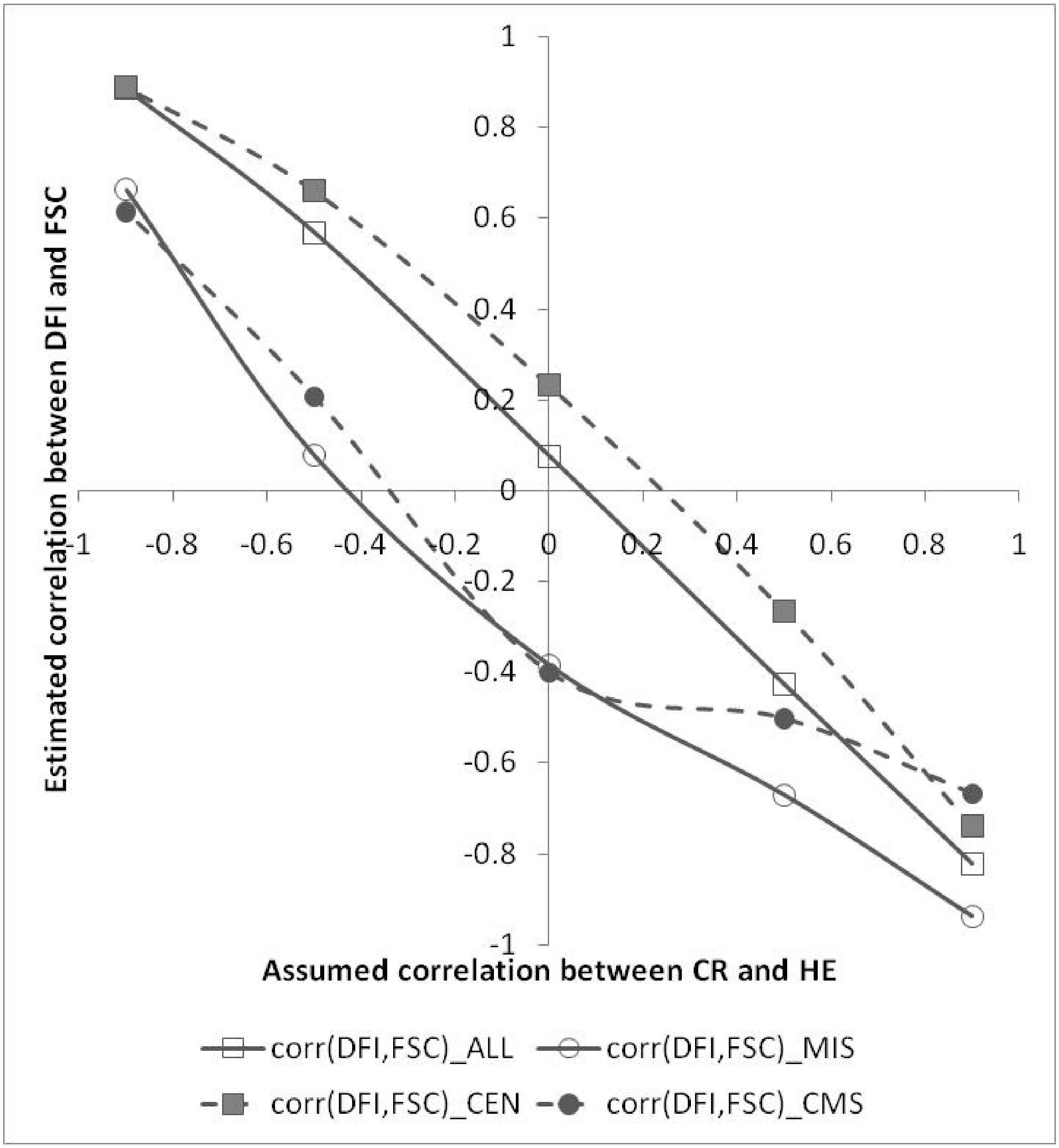

Figure 3.8. Estimated genetic correlations between days to first insemination (DFI) and conception rate at first service (FSC).

CHAPTER 4

STUDY ON GENETIC PARAMETERS OF CONCEPTION RATE AND HEAT EXPRESSION RATE OF NEW YORK HOLSTEINS

ABSTRACT

The purpose of this study was to estimate genetic parameters for heat expression rate (HE), conception rate (CR), and days open (DO). As HE is not observed directly, two indirect measures of HE were proposed: HE2 = minimum of 21/service interval (SI) or 1, and HE3 = 0 if SI >25 or 1 if SI ≤25. Field data were obtained from Dairy Records Management Systems, Raleigh, NC, and included milk yield and service records of New York Holsteins. Only records from farms with herd-year size >50 cows and from first-parity cows with sires that had >10 daughters were included, and records were grouped according to random or non-random (synchronized) weekly insemination patterns. The final data set included information for 104,058 cows with 214,203 service records from 2000 to 2003. Traits examined were CR as the binary outcome of each insemination, DO as the interval from calving date to last service date limited to 21 to 250 days, the two indirect HE measures, CR as the binary outcome at first insemination (FSC), and days to first insemination (DFI). Traits analyzed in a bivariate model were DO with HE2 or HE3 and FSC with DFI. The model included fixed effects for herd-year, days in milk, season, daily milk yield, cow age, AI status and random effects for service sire, additive animals, and cow's permanent environment. Estimated heritabilities were 2.7 and 2.8% for CR, 3.7 to 4.5% and 3.4 to 4.0% for DO, 1.4 and 2.4% for HE2, 3.5 and 3.7% for HE3, 5.1 and 3.6% for FSC, 6.4 and 5.9% for DFI for herds with even and uneven distributions of inseminations over a week, respectively. Estimated genetic correlations were −0.66 and −0.46 between DO and HE2, −0.99 and −0.51 between DO and HE3, and 0.09 and −0.34 between FSC and DFI for the two reproductive strategy groups, respectively. Corresponding results from a previous simulation study indicate a moderately positive genetic correlation between CR and HE. Further suitable selection criteria of HE measures are required for different management systems.

Key words: Fertility, Conception rate, Heat expression rate.

INTRODUCTION

For improving conception rate (**CR**), inefficient heat expression has long been the primary managerial concern related to reproductive performance. Morrow et al. (1966) reported a 79% incidence of silent or unobserved estrus at first ovulation in normal animals. Reimers et al. (1985) found that the percentage of erroneous heat expression (i.e., cows were not in or close to estrus when inseminated) ranged from 0 to 60% among dairy herds from 7 states in the northeastern United States. Moreover, the Raleigh Dairy Records Processing Center reported the mean heat expression rate (**HE**) (i.e. heat detection rate) was 38% for 4,550 herds across the United States in 1992 (Heersche and Nebel, 1994). Erroneous heat expression could be an important reason for low CR.

The most frequent indicators of reproductive performance—calving interval (**CI**) and days open (**DO**)—have significantly increased over past 30 years (Olori et al., 2002; Washburn et al., 2002). Studies demonstrated that the unfavorable increase of CI and DO resulted not only from low CR but also from inefficient heat expression (Esslemont and Ellis, 1974b; Lyimo et al., 2000). Barr (1975) confirmed that lost reproductive days were a consequence of missed heats and were highly correlated (0.92) with more DO. Bailie, (1982) also reported that low HE led to longer CI and ultimately resulted in a higher involuntary culling rate.

Strategies for improving HE have focused only on synchronization to regulate estrus cycles (Hansel, 1961) and detection aids for observing heat symptoms (Foote, 1975). After long-term development of synchronization protocols, however, the pregnancy rate (**PR**) per AI was still lower in group of cows with timed AI (44%) than for a group with visual heat detection

(56%) (Stevenson, 2008). Furthermore, dairy producers need more practical and focused methods of detecting estrus because changes in the structure of the dairy industry (e.g., larger herds, fewer laborers, and utilization of estrus detection aids) but have resulted in decreased attentiveness for routine cow observation (Senger, 1994; Law et al., 2009).

In the past, studies on heat expression have emphasized physiology and management. No studies concentrated on improving HE by using genetic selection tools because of a lack of direct records for HE in data recording systems. Following a simulation study by Pecsok et al. (1994) in which DO was estimated based on estrus expression probability and AI conception probability, Huang (2009) conducted a simulation study in which different measures of HE were derived from other variables to estimate the genetic correlation between HE and CR. In that study, author found that the genetic correlation from some bivariate models could moderately indicate the genetic correlation between HE and CR. The purpose of this study was to apply different measures of HE to estimate genetic parameters for HE, CR and DO based on field data.

MATERIAL AND METHODS

Data

Animal Care and Use Committee approval was not obtained for this study because field data were used. Holstein insemination and production records in New York State from 2000 to 2003 were obtained from Dairy Record Management Systems, Raleigh, NC. All records were required to have cow ID, birth date, calving date, service date, parity number, and first three test-day milk yields. Records for inseminations that were repeated later within 3 days or were before 21 days in milk (**DIM**) or after 250 DIM were excluded. Only records from farms with herd-year size >50 cows and from first-parity cows with sires that had >10 daughters were included. A subsequent calving record was required to confirm a successful conception; therefore, the outcome of last insemination and DO were treated as censored for cows without a subsequent calving record. Daily milk yield was represented by the mean yield for the first three test days. The final data set included 214,203 service records for 104,058 Holstein cows from 1,621 New York farms.

The numbers of service records on each week day were counted within herd-year, and a χ^2 test was used to examine insemination distribution during the week as an indicator of estrus synchronization. Herds were classified as having either an even or uneven distribution of inseminations during the week. Data statistics based on even and uneven weekly insemination distributions for herds are in Table 4.1.

Statistical analyses

Analyzed traits included CR, DO, 2 HE measures, CR at first service (**FSC**), and days to first insemination (**DFI**). The CR was the binary outcome of each insemination, DO was the interval between calving and last service limited to 21 to 250 days, FSC was the binary outcome of first insemination, and DFI was the interval from calving to first insemination. Detailed definitions of different indirect HE measures were described by Huang (2009). For this study, HE for each service record based on service interval (**SI**), which is the interval between two adjacent inseminations and an estrus cycle of 21 days (**HE2**) was

$$\mathrm{HE2} = \begin{cases} \min\left(\frac{21}{\mathrm{DFI}}, 1\right) & \text{first service} \\ \min\left(\frac{21}{\mathrm{SI}}, 1\right) & \text{later services} \end{cases}$$

and HE based on success or failure of heat detection as a function of SI (**HE3**) was:

$$\text{HE3} = \begin{cases} \text{missing} & \text{first service} \\ 0 & \text{if SI} > 25 \\ 1 & \text{if SI } \leq 25 \end{cases}$$

The SI for defining HE3 was set to 25 days because mean SI was >21 days under field conditions (Table 4.1).

All six traits were analyzed with a bivariate linear or threshold-linear animal model defined as

$$\begin{bmatrix} \mathbf{l} \\ \mathbf{y} \end{bmatrix} = \mathbf{Xb} + \mathbf{Ws} + \mathbf{Z_1u} + \mathbf{Z_2p} + \mathbf{e}$$

where **l** = vector of unobserved liabilities for service records and HE3 from a binary outcome (no conception or conception); **y** = vector of observations for DO, DFI, and HE2 as continuous traits; **b** = vector of fixed effects for herd-year, calving month (for DO), service month (for repeated records), DIM (for repeated records), service types (for CR), and calving age and mean of first three test-day milk yields as covariate; **s** = vector of random sire effects (used only for CR); **u** = vector of random animal effects; **p** = vector of random permanent environmental effects for cows; **X, W,** $\mathbf{Z}_1$**, and** $\mathbf{Z}_2$ = incidence matrices for **b**, **s**, **u**, and **p**, respectively; and **e** = vector of random residual effects. Variances were defined as

$$\text{var}\begin{bmatrix} \mathbf{s} \\ \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{S} \otimes \mathbf{I}_\mathrm{s} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G} \otimes \mathbf{A}_\mathrm{u} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P} \otimes \mathbf{I}_\mathbf{p} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \otimes \mathbf{I}_\mathrm{e} \end{bmatrix}$$

where $\mathbf{G} = \begin{bmatrix} g_1^2 & g_{12} \\ g_{21} & g_2^2 \end{bmatrix}$; $\mathbf{P} = \begin{bmatrix} 0 & 0 \\ 0 & p_2^2 \end{bmatrix}$; $\mathbf{R} = \begin{bmatrix} e_1^2 & 0 \\ 0 & e_2^2 \end{bmatrix}$ or $\begin{bmatrix} e_1^2 & e_{12} \\ e_{21} & e_2^2 \end{bmatrix}$; $\mathbf{A}_\mathrm{u}$ = numerator relationship matrix ; $\mathbf{I}_\mathrm{x}$ = identity matrix for effect x.

Variance components were estimated with the GIBBS2F90 program (Misztal et al., 2002) for continuous traits and THRIGIBBS1F90 program (Misztal et al., 2002) for binary traits via a Bayesian approach using Gibbs sampling for linear and threshold models. For each analysis, 100,000 Gibbs samples were discarded as burn-in, and every tenth sample from the following 100,000 samples was saved to calculate posterior means and standard deviations for (co)variance component, correlation, and heritability estimates.

RESULTS AND DISCUSSION

The herd restrictions of >50 herd-year size and >10 daughters per sire were imposed to limit data to those from large farms. An uneven distribution of inseminations during the week was expected to indicate that estrus was being synchronized as weekly inseminations typically are distributed uniformly without synchronization. Herds with an even distribution for weekly inseminations had longer SI, less number of services per conception and slightly more DO (Table 4.1), which supports the assumption that an even distribution of weekly inseminations indicates natural heat expression without synchronization.

Huang (2009) found an extremely high genetic correlation (−0.99) between DO and CR with a bivariate model. With field data, the genetic correlations were also −0.99 (not shown) for both reproductive strategy groups. The extremely high genetic correlation between DO and CR is an artifact of censoring, truncation, and non-normal distribution of both DO and CR. With a single-trait repeatability animal model, the estimated heritability of CR (0.027) did not differ between the two reproductive management groups, but herds with an even distribution for weekly inseminations had almost two-fold smaller variation of service sires (0.079 vs. 0.138) (Table 4.2) and higher repeatability (0.1305 vs. 0.062). The large variation for service sires under even weekly inseminations was unexpected as other studies reported only slight CR variance for service sires (Boichard and Manfredi, 1994; Weigel and Rekaya, 2000; Clay and McDaniel, 2001) but could have resulted from natural services that were included in this study.

Table 4.3 to 4.5 show means and standard deviations of genetic parameters from bivariate animal models for DO with HE2 or HE3, and for FSC with DFI. Estimated heritability of DO ranged from 0.034 to 0.045, which agrees with heritability estimates from other studies (Raheja et al., 1989b; Hayes et al., 1992; Pryce et al., 1997; Dematawewa and Berger, 1998; Abdallah and McDaniel, 2000). Residual variance of DO was larger for herds with uneven weekly inseminations; the variance of DO strongly depends on the mean (Oseni et al., 2004). However, comparison of variance components may be limited value because no clear herd indicator was available for actual estrus synchronization or other managerial decisions.

The HE2 associated with the first service could be biased because DFI was used instead of SI and DFI may include an unknown voluntary waiting period (**VWP**). Moreover, first-service HE2 cannot be considered as missing data because of restrictions of the data. Genetic correlations between DO and HE2 are −0.66 for herds with even weekly inseminations and −0.46 for herds with uneven weekly inseminations (Table 4.3). The negative genetic correlations between DO and HE2 indicate a moderately positive genetic correlation between CR and HE according to the simulation study of Huang (2009). Herds with even weekly inseminations had a higher genetic correlation between DO and HE2 but a smaller heritability of HE2 (0.014) than did herds with uneven weekly inseminations (0.024). That finding indicates that herds with uneven weekly inseminations (i.e. timed AI) have a lower genetic correlation between heat expression and conception because of easier detection of estrus following hormone administration.

Similar to HE2, HE3 (the binary outcome for heat expression depended on a threshold SI of 25 days) can be biased for first service because of unknown VWP. However, that bias may be accounted for by considering first-service records as missing, which can be analyzed with

THRIGIBBS1F90 (Misztal et al., 2002). The genetic correlation between DO and HE3 was −0.99 for herds with even weekly inseminations compared with −0.51 for herds with uneven weekly inseminations (Table 4.4). Again, the negative genetic correlations between DO and HE3 for herds with uneven weekly inseminations suggest the moderately positive genetic correlation between CR and HE based on simulation study by Huang (2009). Similar to HE2, the genetic correlation between DO and HE3 for herds with uneven weekly inseminations was lower than for herds with even weekly inseminations (i.e., natural head expression). The genetic correlation between HE and CR would be expected to have greater value for herds with natural heat expression than those with estrus synchronization and timed AI. Estimated heritabilities for HE3 were similar for both weekly insemination distributions (0.035 and 0.037) and higher than estimate of HE2, likely because of the missing measure of HE3 at first service.

The bivariate animal model was also applied for FSC and DFI because genetic correlations for first-service HE measures, which were functions of DFI and, therefore, had unknown VWP, were very different for herds with even and uneven weekly insemination distributions because of computing limitations. Estimated genetic correlation between FSC and DFI was 0.095 for herds with even weekly inseminations and −0.345 for herds with uneven weekly inseminations (Table 4.5). The moderately negative genetic correlation between FSC and DFI for herds with uneven weekly inseminations suggests a moderately positive genetic correlation between CR and HE following the simulation study of Huang (2009). That result agrees with those for HE measures for herds with uneven weekly inseminations; selecting on CR can moderately improve HE in herds with hormone administration. However, that inference does not apply to herds with even weekly inseminations, for which the genetic correlation between CR and HE varied dramatically between 0 to 100% for different HE measures and models. That correlation range may result from more DFI and greater DFI variation for herds with even weekly inseminations compared with herds with unevenly weekly inseminations (Table 4.1). Genetic correlation between CR and HE is large but hard to interpret for herds without hormone regulation, and more sophisticated models are required for further study.

Results of Huang (2009) for DO, CR, and HE based on simulated data indicated large variability for estimated correlations between fertility and heat expression measures for data subsets with either missing or censored observations. The most accurate estimates were between CR and HE2 (or HE3), which could estimate the true genetic correlation between CR and the underlying HE. Although, the bivariate model with CR and indirect HE measures could not be applied to field data because cows were not inseminated based on a 21-day estrus cycle as was done for simulated data, a bivariate model with DO and an indirect HE measure can be applied to field data and indicate the genetic correlation between CR and HE. However, further model refinements are necessary for unambiguous determination of the genetic correlation between CR and HE.

The two herd groups for reproductive strategy were distinguished according to weekly insemination distributions and not an actual managerial variable. However, the estimated genetic correlations between DO and HE measures and other genetic parameters could be due to management differences. Genetic correlations of DO with HE2 and HE3 confirmed a moderately positive genetic correlation between CR and HE. Estimated heritabilities of HE measures ranged from 0.014 to 0.037, which indicate sufficient genetic variation in HE to be potentially useful. However, different SI for HE3 should be considered when this measure is used for different management systems. Consequently, HE can be improved not only by regulating estrus cycles and estrus detection aids but also through a genetic selection program. It also can be included in a reproductive index with other variables such as DO, CR, and SI.

In this study, all variation in insemination intervals was treated as due to heat expression. In fact, a large part of such variation is due to early embryonic mortality (Ryan et al., 1993). Also, the meaning of HE in synchronized farms is not clear. This study constituted an initial effort into finding genetic parameters for components of fertility, and results from this study should be interpreted with caution.

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Table 4.1. Data statistics for herds based on even and uneven distribution of inseminations over a week*.

	Weekly insemination distribution	
	Even	Uneven
Cows (no.)	36,333	67,825
Service records (no.)	66,725	147,478
Herds (no.)	976	645
Days open	131.39 (57.79)	124.35 (58.24)
Services (no.)	1.84 (1.17)	2.17 (1.41)
Service interval (days)	40.04 (26.02)	38.16 (23.94)
Days to first service	97.69 (43.87)	79.54 (31.16)
Calving age (months)	26.42 (3.53)	25.12 (3.03)
Daily milk yield (kg)	30.15 (5.94)	31.77 (6.33)

*Standard errors in parentheses

Table 4.2. Means (and standard deviations in parentheses) for genetic parameters of conception rate by distribution of herd inseminations over a week.

Parameter	Weekly insemination distribution			
	Even		Uneven	
Additive	0.034	(0.010)	0.034	(0.010)
Service sire	0.079	(0.009)	0.138	(0.007)
Permanent environment	0.122	(0.021)	0.035	(0.014)
Residual	1.000		1.000	
Heritability	0.027	(0.015)	0.028	(0.005)

Table 4.3. Means (and standard deviations in parentheses) for genetic parameters of days open (DO) and heat expression rate for each service record (HE2) by distribution of herd inseminations over a week.

	Weekly insemination distribution							
	Even				Uneven			
Parameter	DO		HE2		DO		HE2	
Additive	106.54	(19.67)	−0.218[a]	(0.043)	104.92	(17.06)	−0.196[a]	(0.028)
	−0.659[b]	(0.116)	0.001	(0.0002)	−0.462[b]	(0.064)	0.002	(0.0002)
Permanent environment			0.001	(0.0003)			0.002	(0.0002)
Residual	2,746.69	(28.22)	0.076	(0.0004)	2,980.66	(19.39)	0.069	(0.0003)
Heritability	0.037	(0.007)	0.014	(0.003)	0.034	(0.005)	0.024	(0.002)

[a] Genetic covariance of DO and HE2.

[b] Genetic correlation of DO and HE2.

Table 4.4. Means (and standard deviations in parentheses) for genetic parameters of days open (DO) and heat expression rate based on a binary outcome for each service record (HE3) by distribution of herd inseminations over a week.

	Weekly insemination distribution			
	Even		Uneven	
Parameter	DO	HE3	DO	HE3
Additive	129.40 (26.41)	−2.154[a] (0.362)	122.22 (18.71)	−1.148[a] (0.328)
	−0.990[b] (0.010)	0.037 (0.007)	−0.513[b] (0.096)	0.040 (0.008)
Permanent environment		0.006 (0.004)		0.056 (0.010)
Residual	2,727.21 (30.64)	1.000	2,966.00 (22.10)	1.000
Heritability	0.045 (0.009)	0.035 (0.006)	0.040 (0.006)	0.037 (0.009)

[a] Genetic covariance of DO and HE3.

[b] Genetic correlation of DO and HE3.

Table 4.5. Means (and standard deviations in parentheses) for genetic parameters of conception rate at first service (FSC) and days to first insemination (DFI) by distribution of herd inseminations over a week.

	Weekly insemination distribution			
	Even		Uneven	
Parameter	FSC	DFI	FSC	DFI
Additive	0.056 (0.014)	0.213[a] (0.356)	0.037 (0.007)	−0.399[a] (0.148)
	0.095[b] (0.160)	90.66 (15.88)	−0.345[b] (0.115)	36.01 (5.75)
Residual	1.000	4.34[c] (0.44)	1.000	1.62[c] (0.21)
	0.116[d] (0.012)	1,334.15 (17.33)	0.059[d] (0.008)	742.12 (6.46)
Heritability	0.051 (0.012)	0.064 (0.011)	0.036 (0.007)	0.059 (0.008)

[a] Genetic covariance of FSC and DFI.

[b] Genetic correlation of FSC and DFI.

[c] Residual covariance of FSC and DFI.

[d] Residual correlation of FSC and DFI.

CHAPTER 5

CONCLUSIONS

Reproductive performance has become the primary concern of dairy breeders and researchers during the last decade. Several fertility traits have been extensively studied including: calving interval, days open, days to first insemination, pregnancy rate, conception rate, conception rate at first service, non-return rate, and number of services per conception. Current heritabilities for fertility traits are generally low and range from 1 to 10% depending on the definition of the trait, the information available, and the methodology used for analysis. If the intent is to enhance reproductive performance comprehensively, gamete formation and embryonic and fetal development and maintenance should be considered in addition to the fertilization stage. However, no direct information on heat expression and embryonic mortality is available in the current record system.

Three indirect measures of heat expression were derived from days open as a function of voluntary waiting period, heat expression rate, and conception rate. The two repeated measures of heat expression were ideally indicative of known assumed genetic correlations between conception and heat expression rates when paired with conception rate under a regular 21-day estrus cycle, but results were not similar for bivariate models with days open. When the two repeated measures of heat expression were applied to large sets of field data, however, the estimated genetic correlation between days open and measures of heat expression indicated a moderately positive genetic correlation between conception and heat expression rates, but the two measures did not work well in bivariate models with conception rate. The other paired fertility traits for first insemination only also could be an indicator of the correlation between conception and heat expression rates. Their advantage is early estimation of the correlation, but they cannot reveal relationship trends over days in milk. In addition, inseminations that are not distributed evenly during the week may indicate that estrus synchronization and timed AI are being used in the herd.

Fertility traits are very complicated, confounded with each other, and strongly influenced by data quality. The genetic correlation between days open and conception rate was estimated to be −0.99 regardless of the magnitude and sign of assumed parameters for simulated data as well as for field data, an indication that the correlation is affected not only by other fertility traits but also by raw data quality. The genetic correlation between days open and conception rate cannot be a reliable fertility guide under current information and methodologies. However, the two indirect measures of heat expression are moderately informative when combined with days open. The results indicated a moderately positive genetic correlation between conception and heat expression rates. More comprehensive data and sophisticated models and methodologies are required to study the interaction of multiple factors for reproductive traits.

APPENDIX[1]

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[1] Huang, C., I. Misztal, S. Tsuruta and T. Lawlor. Interbull Bul. 37:156-160.

Methodology of Evaluation for Female Fertility

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Introduction

Female fertility is a complex trait. It is affected by time to first heat, voluntary waiting period, heat detection rate, conception rate, embryo survival and fetus mortality. All of these component traits are functions of genetics management and seasonal effects. Some of these traits behave differently under estrus synchronization than under a natural heat. Additional issue is an interrupted breeding season due to implementation of pasture systems or hot weather.

There are many traits and methods used for the evaluation of fertility (Jamrozik *et al.,* 2005). They include non-return rate (NR) at 45 to 90 days, days open (DO) analyzed by several models, outcomes of services, etc. Some of the traits are binary or categorical, and some are censored.

It is desirable that an evaluation for fertility provide accurate predictions as early as possible with a good utilization of data. There are many factors that may make an evaluation inaccurate. Long voluntary waiting periods or voluntary non-breeding may be misinterpreted as poor fertility. Much larger variance of DO in farms with poor fertility may result in higher proportion of good bulls used in farms with poor fertility; voluntary non-breeding during hot weather results in bimodal days open (DO) (Oseni *et al.,* 2004). Poor heat detection or slow return to heat, e.g., "phantom cow syndrome" (Cavalieri *et al.,* 2003), and subsequently longer service intervals may result in misleading data.

Analysis of Field data on fertility is often limited in scope by the amount of missing information. In particular, information on heat detection or embryo mortality is usually unavailable. Therefore, data simulation is a useful tool for comparison of methods under different circumstances, e.g., as in Schneider *et al.* (2005, 2006). Drawbacks of simulations include unrealistic outcomes with unrealistic assumptions, and favoring of models under which the data was simulated.

The purpose of this study was to compare the ability of different models, via data simulation, to correctly analyze female fertility.

Materials and Methods

Data

A threshold-liability model was used to generate our simulated data. The liability to conception η in a single service was modeled as:

$$\eta_{ijklm}=\mu+\text{month}_i+\text{milk}_j+\text{dim}_k+s_l+e_{ijklm}$$

where μ is a mean, month is an effect of month of service, milk is the effect of class of milk level, dim is the effect of days-in-milk class, and s is the effect of sire Any breeding service with $\eta >0$ would result in a pregnancy.

All first services occurred at 69 d DIM. If it was not successful, the next service was generated 21 d later, up to 250 d DIM.

The heritability was set to 2%. The simulation involved 55,000 cows and 1000 sires, and the average number of services per cow was 4.2. The average conception rate was set at 22%; it decreased with the level of production, decreased during the summer months, and increased with DIM. Proportion of cows becoming pregnant by 150, 200 and 250 d was 46%, 74% and 88%, respectively.

Methods for analysis of simulated data

The following methods were used:

RPT - Repeatability model of outcomes of services, similar to Boichard *et al.* (1997) or Averill *et al.* (2006), was used.

Each insemination was considered a separate event under the RPT model allowing for considering fixed effects specific to each service. Genetic and permanent environmental covariances for insemination success at different times were assumed to be constant. Both a threshold and linear model was analyzed

NR - Non-return rate; measures the success of a breeding by noting the occurrence or lack of occurrence of any additional breeding after X number of days. In our study, X number of days was 21, NR 21 was equivalent to the success of the first insemination.

COX - Cox proportional hazards model on days open.

The proportional hazards models assume a smooth flow of time, as in life. In such a case, it accounts for non-normal distribution and censoring. A loss of efficiency is likely if intervals between inseminations are not equally spaced. Also, this model as implemented by Ducrocq and Soelkner (1998) cannot easily be used with an animal or multiple trait model.

DOx - Days open with censored records at day x treated as missing

DOxPEN - Days open with censored records at day x treated as equal to x (penalized model).

DOx/CS – a bivariate model of DOx and calving success (CS); calving success was set to 1 if there was pregnancy by day x, and it was 0 otherwise (Arnason, 1999; Foulley, 2004).

Implementation and computations

The RPT model included all the effects used in the liability calculations. The remaining models used the effects of months at calving, milk and sire. Computations in the COX model involved the survival kit by Ducrocq and Soelkner (1998).

All models were evaluated by the correlation between simulated and predicted sire effects. Thresholds models were used whenever appropriate. Computations with the RPT model were also repeated using the linear model.

Results

The table below provides correlations between simulated and predicted sire effects (R), and estimated heritabilities (h^2).

Method	R	h^2
RPT	0.559	2.01%
RPT[1]	0.556	0.88%
NR	0.331	0.42%
COX	0.538	1.86%
DO150		
DO200	-0.300	0.83%
DO250	-0.419	1.73%
DO150PEN	-0.444	1.32%
DO200PEN	-0.518	2.55%
DO250PEN	-0.550	3.21%
DO150/CS[3]	-0.464	0.08%
DO200/CS[3]	-0.543	1.02%
DO250/CS[3]	-0.552	1.93%

[1]linear model; [2] estimated heritability close to 0; [3]results for DO

The highest correlation as well as heritability close to that used in the simulation was obtained with the RPT threshold model. This was expected because this model was close to the one used to simulate the data. In particular, it was the only one that accounted for environmental differences during each service. Substituting the threshold by the linear model resulted in a slight decrease in correlation and less than half of the heritability estimates. In a study by Ramirez-Valverde *et al.* (2001), the threshold model showed the greatest improvement with an animal bivariate model but little improvement with the sire model. Either RPT model ignores the length of time between inseminations making them a desirable choice when a period of voluntary non-breeding occurs. A potential source of bias is that poor heat detection may provide inflated estimates of fertility for cows that have poor expression of estrus.

With the NR21 model, the correlations were low. This was due to low probability of conception for a single service. In such a case, NR21 has low data utilization. Selecting the most appropriate time interval may be dependent upon the average level of fertility. With low fertility data (involving poor heat detection) several breeding opportunities may be needed to determine that an earlier insemination was unsuccessful. Ravagnolo and Misztal (2002) found that in Florida, where the service intervals are long, the heritability of NR was only 0.6% at 45 d but increased to 5.3% at 90 d. NR at 90 d may be unsuitable for regions with good fertility

The COX model resulted in the correlation below those of several other models. While this model accounts well for censoring, it was not the model used in the simulation.

DO is an easily measurable trait, however it can be biased by different voluntary waiting periods, unequal variances due to different levels of fertility, and periods of voluntary nonbreeding. Some of these problems can be mitigated by a careful selection of contemporary groups and an adjustment for heterogeneous variances

All DO models showed increased heritability and correlations with increasing x, as expected. Methods that analyze DO take censoring into account by either assuming truncation or stochastic censoring. With truncation censoring (DOxPEN, COX), it is implicitly assumed that given enough time the cow will conceive. With stochastic censoring, calving success is correlated, but is not the same trait as DO. In particular, this model allows some cows to never conceive. In beef cattle under grazing system, DO/CS provided much more accurate prediction than DOxPEN (Urioste *et al.,* 2007).

The most accurate model was DO250/CS followed by DO250PEN, however differences were small. In this case, DO250/CS is similar to a regular censored model that implicitly predicts DO for incomplete records. The advantages of DO250/CS would be higher if censoring were not past day x but stochastic, e.g., partly based on health status.

Gonzalez-Recio *et al.* (2005) found that several models provided nearly identical PTAs despite of different source of information and a different type of accounting for censoring. This can be due to relatively uniform environment for the majority of cows in the study, or the averaging effects where sires are used in a variety of environments. Another possibility is that the component traits of fertility are strongly correlated.

General comments

Next steps in the simulation would involve adding liability to heat detection, age to first service, voluntary waiting periods, voluntary seasonal non-breeding, the animal model, etc. Countries with different levels of genetic ability for fertility, environmental circumstances and management practices will need to experiment with a variety of models before identifying the best choice for their situation.

It would be best to evaluate each component trait of the fertility complex separately. The overall goal of producing a healthy calf is dependent upon a succession of many different events being successful. Poor performance in any one step will lead to a poor outcome. However, data recording on estrus detection or embryo mortality is often lacking. Some indirect measures of several component traits may be obtained by comparing PTAs from different methods.

Conclusions

Most models are likely to provide robust evaluations if sires are well sampled across environments or the majority of data originates from farms with similar environmental conditions. If data are available and heat detection is not a problem, perhaps the best evaluation would be to analyze each service record (RPT). If heat detection is an issue, a separate evaluation (e.g., DO/CS that accounts for stochastic censoring) would provide extra information. Evaluation under highly variable environments would require careful selection of fixed effects and possibly adjustments for heterogeneous variances.

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