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Genetic analysis of fertility in Brown Swiss dairy cattle

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Riassunto

La perdita di efficienza riproduttiva nel settore della bovinicoltura da latte è ormai un dato di fatto. Diversi studi hanno dimostrato come, a seguito dell'incremento in produttività avuto negli ultimi 40 anni, la fertilità si sia drasticamente ridotta, con circa un decennio di ritardo rispetto alla produzione.

Sul piano del miglioramento genetico le strategie per invertire questa tendenza sono diverse. Bisogna prima di tutto considerare quanto il valore genetico additivo dei riproduttori pesi sulle loro prestazioni, dato che da ciò dipende la possibilità o meno di miglioramento genetico di quel carattere attraverso le tradizionali vie selettive. Non bisogna neanche trascurare le relazioni che, sempre a livello genetico, intercorrono tra i caratteri di fertilità e quelli fino ad oggi oggetto di selezione, relazioni che difficilmente saranno favorevoli dato che è stata proprio la selezione degli ultimi decenni ad deprimere la fertilità.

I caratteri di fertilità però non sono di facile acquisizione. È necessaria la puntuale registrazione delle singole inseminazioni, e ciò comporta una accurata organizzazione del sistema di controllo, nonché costi aggiuntivi rispetto ai normali controlli funzionali. Per di più i parametri di fertilità sono molto suscettibili ad errori o lacune nella registrazione. Una possibile soluzione è quella di impiegare caratteri correlati con la fertilità che però siano di più facile raccolta. La condizione di stato corporeo della vacca (o Body Condition Score) è stata più volte presa in considerazione come carattere predittore di fertilità.

Quando si parla di fertilità di solito si pensa ad un'efficienza riproduttiva femminile. In effetti, è stato sulle vacche che si è prima e maggiormente riscontrato il problema della difficoltà al concepimento e mantenimento della gravidanza. Tuttavia, il ruolo degli individui di sesso maschile, nello specifico i tori fecondanti, non può essere trascurato. Nei sistemi a prevalente inseminazione strumentale come quelli delle razze specializzate da latte pochi riproduttori maschili sono messi in condizione di fecondare migliaia di vacche, e, benché ci siano dei controlli sulla qualità del materiale seminale messo in circolazione, la relativa fertilità di ogni toro ha un impatto rilevante sulla fertilità generale della popolazione. Ecco che la fertilità maschile diventa di importanza, ed una sua misurazione con dati di campo può aiutare a comprendere meglio un suo possibile ruolo nella determinazione dell'efficienza riproduttiva della popolazione oggetto di studio.

Per lo svolgimento di questa tesi si è preso in esame la popolazione di razza Bruna Italiana allevata nella provincia di Bolzano. In questo contesto è in funzione un efficiente schema di raccolta informazioni che permette la registrazione delle inseminazioni effettuate con buona attendibilità.

Prima è stato creato un archivio contente tutti gli interventi fecondativi ritenuti attendibili, coprendo un arco temporale dal 1999 al 2008. Per la fertilità maschile, da questo archivio si sono estratte le inseminazioni effettuate con seme di soli tori di razza Bruna Italiana. Per ognuna di queste inseminazioni si è considerato il non-ritorno a 56 giorni ed il concepimento (validato sulla base della ipotetica lunghezza di gravidanza).

Sempre dall'archivio generale si sono create le diverse misure di fertilità femminile, siano essere intese come intervallo di tempo tra due eventi significativi per la riproduzione (intervalli tra il parto, la prima inseminazione, il concepimento) o come indicatori di successo degli interventi fecondativi (numero di inseminazioni per concepimento, non-ritorno dopo la prima inseminazione, concepimento alla prima inseminazione). Inoltre, i caratteri produttivi e le misure di condizione corporea della vacca che vengono ufficialmente raccolte dalla associazione di razza a livello nazionale (ANARB) sono state unite ai caratteri di fertilità.

Il primo contributo si incentra sulla quantificazione della variabilità genetica additiva per la fertilità da parte maschile. Dal momento che la selezione per la fertilità dei riproduttori maschili viene fatta per via fenotipica, lo studio si è incentrato sulla predizione del valore genetico di tali riproduttori per la loro stessa fertilità, attraverso il confronto di diversi modelli predittivi.

Data la natura delle variabili, i modelli a soglie sono considerati più appropriati, ma si è voluto comunque provare anche l'efficacia dei modelli lineari, che assumono la distribuzione continua e normale della variabile. Si è assunto che fosse l'embrione, che si stava instaurando, a rappresentare l'individuo con fenotipo. Sono quindi stati provati degli "animal models" che dei "sire models". Gli effetti casuali ambientali e genetici, sono stati inseriti sequenzialmente all'interno di queste 4 combinazioni di modelli.

Per ogni modelli, applicato ad entrambe le variabili, si sono calcolate componenti di varianza ed ereditabilità. Poi si è diviso il dataset in due parti, su base temporale, in modo da stimare gli indici genetici dei tori su di un dataset ed usarli per predire la restante parte delle osservazioni. Il datset di calibrazione comprendeva gli anni dal 1999 al 2005, mentre il dataset riguardante i restanti tre anni è stato usato come validazione. Le componenti di varianza estratte sono risultate basse, ma un certo grado di somiglianza a livello genetico è emerso dalle analisi. Le ereditabilità infatti sono rimaste sotto i dieci punti decimali, risultato che è sicuramente più incoraggiante dei quelli trovati in bibliografia. Diverse statistiche non parametriche hanno dimostrato come, benché non esista una sostanziale differenza tra i modelli lineari e quelli a soglie, gli animal models davano predizioni relativamente più accurate, e anche il confronto tra le specifiche dei modelli sembra favorire i quelli più compressi. In generale però le predizioni sono tendenzialmente povere, il che riflette le basse componenti di varianza genetica additiva stimate.

Il secondo contributo della tesi si pone come obbiettivo di quantificare la variabilità genetica della popolazione in esame da parte femminile. I caratteri presi in esame sono quelli più comuni nella valutazione genetica per la fertilità (intervallo tra parto e primo servizio, intervallo tra primo servizio e concepimento, intervallo tra parto e concepimento, numero di inseminazioni al concepimento, concepimento alla prima inseminazione, non-ritorno a 56 giorno dopo la prima inseminazione) ed i più importanti caratteri produttivi (produzione di latte al picco di lattazione, produzione di latte nell'intera lattazione, durata della lattazione, e percentuali media di grasso e proteina nella lattazione). Tutti i caratteri sono stati considerati indipendentemente dall'ordine di parto su cui erano registrati. Inoltre, i caratteri riproduttivi intesi come intervalli sono stati suddivisi in classi di 21 giorni, con lo scopo di ripercorrere il ciclo estrale della vacca e misurare il periodo come numero di cicli estrali. Diversi modelli misti di tipo 'sire model' sono stati impiegati. Per analizzare le differenti variabili ci si è avvalsi di modelli lineari e modelli a soglie (threshold model). Questi ultimi operano una trasformazione della distribuzione della variabile in oggetto da discreta a continua, creando una variabile, che si intende latente, sulla quale poi viene applicato il modello misto. Inoltre, per tenere conto di possibili perdite di informazioni dovute a riforma degli animali (quantificazione dell'intervallo tra il parto ed il concepimento per vacche che non presentano un successivo parto) si sono utilizzati modelli 'censored'. Questi modelli sono capaci di simulare una valore del parametro incrementato a partire dal valore registrato (data augmentation). Sono stati creati anche dei modelli bivariati per la quantificazione della correlazione genetica tra i caratteri produttivi e quelli riproduttivi. La metodologia impiegata si basa su inferenze costruite sulla distribuzione a posteriori dei parametri stimati (inferenza Bayesiana).

I risultati hanno evidenziato una componente genetica additive della fertilità bassa ma presente. Le ereditabilità per i caratteri riproduttivi sono infatti comprese tra lo 0.03 e lo 0.08. I caratteri produttivi hanno mostrato ereditabilità relativamente più alte, pur rimanendo comunque sotto lo 0.2. In generale, i caratteri riproduttivi misurati come intervalli di 21 giorni hanno dato ereditabilità più alte dei corrispettivi considerati continui. Le correlazioni genetiche tra i caratteri riproduttivi evidenziano che non è banale considerare l'una o l'altra misura di fertilità, essendo quasi sempre medio-alte, ma non uguali ad 1. Le correlazioni tra i caratteri produttivi e riproduttivi confermano la relazione negativa tra fertilità e produzione.

Alla luce dei risultati di questo studio, si capisce come qualora si voglia inserire la fertilità tra i caratteri obbiettivo di selezione non ci si può aspettare una risposta correlata positiva con quelli produttivi, e viceversa. Le ereditabilità trovate confermano però che la selezione per la fertilità è possibile, nonostante il progresso genetico atteso rimanga comunque modesto.

Nel terzo contributo si è invece considerato che il peso dei vari fattori che condizionano la fertilità femminile potesse variare con l'ordine di parto su cui questa si manifesta. Le variabili già analizzate nel precedente capitolo sono state analizzate come caratteri differenti a seconda che considerassero manze vergini (esclusi i caratteri che considerano un parto precedente), vacche in prima lattazione, e vacche in seconda lattazione. È stata considerata la produzione di latte nella prima lattazione come termine di paragone per il rapporto con i caratteri produttivi. La metodologia impiegata è del tutto simile a quella del primo capitolo.

I risultati indicano che per quanto la fertilità in prima e seconda lattazione possa essere considerata come un unico carattere, la fertilità misurata sulle manze vergini è un carattere sostanzialmente diverso. Per di più, la produzione in prima lattazione mostra il consueto antagonismo con la contemporanea fertilità, mentre le correlazioni con la fertilità della manza sono pressoché nulle. Se però è la fertilità della vacca in lattazione ad essere quella che ha maggiormente risentito della perdita negli ultimi decenni, ed è di questa che si vuole arrestare il peggioramento, misurare la fertilità sulla manza non potrebbe dare i risultati sperati. Tuttavia, le valutazioni genetiche sulla fertilità delle manze comporterebbero un notevole risparmio in termini di tempo dato che sarebbero disponibili con largo anticipo rispetto a quella sulle vacche primipare.

Il quarto contributo si è posto l'obbiettivo di verificare se la misura di condizione corporea delle vacche possa essere un buon carattere strumento per la selezione indiretta per la fertilità femminile. Sulla razza Bruna Italiana viene registrato, con una unica misura, questo carattere sulle vacche primipare, nei primi 180 giorni di lattazioni. Questa misura di condizione corporea è stata messa in relazione con la fertilità e produzione contemporanee (in prima lattazione), e con la fertilità della seconda lattazione. Anche per questo studio la metodologia usata è del tutto simile a quella dei capitoli precedenti.

Sulla base dei risultati ottenuti la condizione di stato corporeo delle vacche primipare, benché negativamente correlata alla contemporanea produzione, non appare fortemente correlata con la contemporanea fertilità, soprattutto con i caratteri di intervallo. Tuttavia, si nota come la condizione corporea sia più legata ai caratteri riproduttivi di intervallo in seconda lattazione. È da evidenziare comunque, quanto l'ispettore incaricato di valutare il caratteri di condizione corporea rappresenti la maggiore fonte di variazione. La misura di condizione corporea delle vacche primipare può rappresentare comunque un valido strumento per operare una selezione indiretta sulla fertilità, e impedirne il successivo peggioramento.

In conclusione la selezione per la fertilità dei bovini da latte sembra possibile. La variabilità genetica esiste, e benché sia bassa, può per lo meno aiutare ad impedire la progressiva erosione di efficienza riproduttiva nei bovini da latte, se considerata nell'indice di selezione complessivo. La scelta degli strumenti di selezione deve essere accurata, in quanto non tutte le misure di fertilità, raccolte in diversi contesti fisiologici possono dare lo stesso risultato. Rimane comunque chiaro che non esiste un carattere che possa esprimere la fertilità femminile nel suo insieme. La condizione corporea delle vacche primipare può essere un valido strumento di selezione indiretta per la fertilità, ma investimenti in questo senso richiedono un miglioramento della ripetibilità e consistenza delle stime, tramite un assottigliamento dell'effetto del valutatore ed una più puntuale misurazione del carattere nelle fasi più significative della lattazione.

La fertilità maschile sembra essere ereditabile. Una sua applicazione in ambito selettivo sembra essere sconsigliabile, ma le modeste componenti di varianza che possono essere estratte sembrano sufficienti a permettere una discriminazione dei riproduttori maschi qualora questi potessero presentare degli scarsi tassi di successo. Questa pratica, fino ad ora portata avanti per via fenotipica, potrebbe vedere l'inclusione dei dati di fertilità di campo. I tori in prova di progenie potrebbero essere valutati, con una accettabile accuratezza sulla loro prestazione riproduttiva futura.

Abstract

The loss of reproductive efficiency in the dairy indistry is now undeniable. Several studies shown that, due to the increase in productivity in recent 40 years, fertility has been drastically reduced, with about a decade of delay on production.

Several animal breeding strategies to reverse this trend have been proposed. We must first consider what the additive genetic value of breeding stock weights on their performance, since it underlay the possibility of genetic improvement for that character through the traditional selection methodology. Moreover, the relationships on the genetic level, existing between the characters of fertility and those currently considered as selection goals should not be neglected. The same relationships are unlikely to be favorable as it was the selection of the last decades to depress fertility.

The characters of fertility, however, are not easy to acquire. The timely recording of single inseminations is required, and this involves an efficient organization of the recording scheme, as well as additional costs to the normal functional controls. Fertility parameters are also very susceptible to errors or deficiencies in the recording. One possible solution is to use characters associated with fertility but are easier to assess. The condition of the cow body fat reserves (or Body Condition Score) has often been considered as a good predictor of fertility.

When it comes to fertility usually think of female reproductive efficiency. In fact, it was the cows that first and foremost have encountered the problem of difficulty in conception and maintaining pregnancy. However, the role of males, specifically bulls used for seme production, can not be neglected. In breeding sceme where artificial insemination is prevailing, as specialized dairy breeds, there are few males used to breed thousands of cows, and, although there are controls on the quality of distributed semen, the relative fertility of each bull has a significant impact on the fertility of the population. Here it becomes of importance, and its measurement with field data can help to better understand its possible role in determining reproductive efficiency in the dairy population.

To carry out this thesis we examined the population of Italian Brown Swiss reared in the province of Bolzano. In this context, is running an efficient scheme for collecting information that allows the recording of inseminations performed with good reliability. First a dataset was created containing all the inseminations considered reliable, covering a period from 1999 to 2008. For male fertility, from this archive we extracted inseminations performed with only registered Brown Swiss bulls semen. For each of these inseminations we considered the non-return at 56 days and conception (validated on the basis of the hypothetical pregnancy length).

From the archive we computed the different measures of female fertility, meant as the time interval between two significant events for playback (intervals between the parturition, the first insemination, and conception) or as indicators of success at insemination (number of inseminations to conception, non-return after the first insemination, conception at first insemination). Furthermore, the productive traits and measures of body condition of cows that are officially collected by the Italian Brown Swiss Breeders' Association on the national basis (ANARB) were merged to fertility characters.

The first contribution focuses on quantifying the magnitude of additive genetic variation for the male fertility. As the selection for male fertility is commonly carried out phenotypically, the study focused on the prediction of genetic value of bulls for their own fertility, through the comparison of different predictive models.

Given the binary nature of the variables, threshold models are considered more appropriate, but we wanted to prove the effectiveness of linear models that assume normal abd continuous distribution of the variable. It is assumed that it was the embryo, which was establishing, to represent the individual with phenotype. We tested both animal models and sire models. The environmental and genetic random effects were sequentially inserted into these 4 combinations of models.

For each model, applied to both variables, were calculated variance components and heritability. Then the dataset is split into two parts, on a time basis, in order to estimate the breeding values of bulls of a dataset and use it to predict the remaining observations. Calibration dataset included years 1999 to 2005, while the dataset about the remaining three years was used as validation. The variance components extracted were low, but a certain degree of similarity at the genetic level emerged from the analysis. Heritability was below 0.1, a result which is certainly more encouraging of those found in the bibliography. Several non-parametric statistics have shown that, although there is not a substantial difference between the linear and thresholds models, the animal models gave relatively more accurate predictions, and also the comparison between the specifications of the models seem to favor the more compressed. In general, however, the predictions tend to be poor, reflecting the low additive genetic variance components estimated.

The second contribution of the thesis has the objective to quantify the genetic variability of the population for female fertility. The traits examined are those most common in the genetic evaluation for female fertility (interval between parturition and first service, interval between first service and conception, interval between parturition and conception, number of inseminations to conception, conception to first insemination, non-return at 56 days after the first insemination) and the most important productive traits (milk production at peak lactation, milk production throughout lactation, length of lactation, and average percentages of fat and protein in lactation). All traits were considered regardless of the parity order on which they were recorded. In addition, the interval traits were divided into classes of 21 days, with the aim to trace the cow's estrous cycle and measure the period as the number of oestrous cycles skipped. Several mixed sire models were used. To analyze the different variables we have used linear models and threshold models (threshold model). These made a transformation of the distribution of the variable in question to continue, creating an underlying latent variable, on which is then applied the mixed model. In addition, to account for possible loss of information due to the reform of the animals (quantification of the interval between calving and conception for cows that do not have a subsequent birth) have used models treating censored informations. These models are capable of simulating a value increased from the value recorded (data augmentation). Were also performed bivariate analysis aimed to quantify the genetic correlation between productive and reproductive characters. The methodology used is based on inferences made on the posterior distribution of the estimated parameters (Bayesian inference).

The results showed an additive genetic component of fertility low but present. The heritability for reproductive traits are in fact the range between 0.03 and 0.08.The productive traits showed relatively higher heritability, although they were still below 0.2. In general, reproductive traits measured as intervals of 21 days gave highest heritability than those deemed to be continuous. The genetic correlations between reproductive traits showed that it is not trivial to consider one or the other measure of fertility, as those were often medium-high, but not equal to 1. The correlations between the productive and reproductive traits confirmed the negative relationship between fertility and production. According to these results, we can infer that considering the fertility traits as selection goal will not lead to a strong response to selection. The heritability found, however, confirm that selection for fertility is possible, despite the expected genetic progress, however, remains modest.

In the third contribution has considered that the weight of the various factors that affect female fertility could vary with birth order on which it is expressed. The variables have already been addressed in the previous section were analyzed with the same methodology but as different traits depending on whether they measured on virgin heifers (excluding the characters based upon a previous calving), first lactation cows, and cows in second lactation. First lactation milk production has been also considered as a reference for the relationship with the production traits. The results indicate that although fertility in first and second lactation can be considered as a single trait, fertility measured on virgin heifers is fundamentally a different character. Moreover, production in first lactation shows the usual antagonism with contemporary fertility, while the correlations with the fertility of the heifers are almost nil. If, however, is the fertility of lactating cows to be the one who has suffered most from the loss in recent decades, and we aim to stop deterioration of first lactation yield, assessing heifer fertility could not give the expected results. However, the genetic evaluations of fertility of the heifers would mean a considerable saving in time because that would be available definitely in earlier than the primiparous cows.

The fourth contribution had the aim to verify if the amount of body fat of cows can be a good trait for indirect selection for female fertility. Body condition score is registered on the Italian Brown breed with a single measurement primiparous cows within the first 180 days of lactation. This measure of body condition has been associated with contemporary fertility and production (first lactation), and with the fertility of second lactation. The methodology used for this study is quite similar to that of the preceding contributions.

Based on these results, the body condition of primiparous cows were negatively correlated to the simultaneous productionbut not strongly correlated with the contemporary fertility, especially with the interval traits. However, body condition was moderately related to second lactation interval traits. I sto be noticed how the inspector (assessing the body condition) to represent the largest source of variation.The measure of body condition of primiparous cows can anyway be a valuable tool to make an indirect selection on fertility, and prevent subsequent deterioration, but more frequent, consistent, and accurate measures of body conditions are needed.

In conclusion, selection for fertility of dairy cattle appears to be feasible. The genetic variability exists, and although it is low, it can at least help to prevent the running erosion of reproductive efficiency in dairy cattle, if considered in the total merit index.The choice of selection tools must be accurate, since not all measures of fertility, collected in different physiological contexts, can give the same result. It remains clear that there is not a traitr able to entirely express the female fertility. The body condition of primiparous cows may be a valid indirect selection tool for fertility, but investments in this direction must improve the repeatability and the consistency of the scores, thinning the effect of the evacuato and providing a more punctual scoring of the body condition in most significant stages of lactation.

The male fertility appears to be heritable. Its application in selection seems to be unwise, but the small components of variance that can be extracted seem to be sufficient to allow discrimination of breeding males if they could present a future lack of success rates. This practice, so far carried out phenotypically, could see the inclusion of the fertility field data. The bulls could be evacuate during first crop, and their future reproductive performance predicted with an acceptable accuracy.

Chapter one

General introduction

The loss of reproductive fitness in dairy cattle

During the last decades reproductive efficiency has become a major concern in animal breeding. Genetic improvement programs in dairy cattle have until recently focused on increasing net profit by increasing gross income per cow, rather than reducing costs of production (Zwald et al., 2004). Strong selection pressure on yield traits coupled with management practices aimed at maximizing production may have resulted in undesirable side effects related to decreased fitness (Hansen, 2000). These concerns have been confirmed by work on reproductive efficiency carried out by several authors (e.g., Lucy, 2001; VanRaden et al., 2004).

Reasons for deterioration of reproductive performance are quite clear nowadays, and the discovery of an additive genetic component for fertility aspects is relatively recent. The first genetic studies on the topic did not provide any evidence of an underlying polygenic effect for reproductive traits. Dumbar and Henderson (1956) reported this sentence as a conclusion of their study on fertility in dairy cattle: '*It seems certain from this study, and from those reviewed briefly, that genetic variance with respect to fertility is essentially zero when fertility is measured by nonreturns to first service, services required per conception, or by length of calving interval*'. The reason of their verdict is likely attributable to the ancient statistical techniques, not efficient in extrapolating genetic variance in such skewed and perhaps non-linear traits. Thirteen years later, Foote (1969) reported different results at the Dairy Cattle Symposium of the American Dairy Science Association. First he stated: '*There are heritable differences in nonreturn rates of sires used in artificial breeding, but the genetic variance appears to be small.*'. Secondarily, he continued: '*Since the genetic relationship of fertility to production is very low, little change in fertility is expected from selecting only for production.*'. The genetic variance for fertility traits was disentangled, but not significant relationship with production traits was found. The ancient statistical methodology was still imputable, but the likely reason of this weak genetic relationship is that it simply did not exist in the middle part of the XX century. Things could have changed across the decades. Bascom and Young (1998) reported that fertility was the primary reason for culling in the United States, and Lucy (2001), in a review on fertility of dairy cattle, showed how herd average milk yield increased considerably since the '70s, followed by an equivalent increase in calving interval and number of services per conception with a 15 years delay. Sometimes the erosion of reproductive efficiency has been attributed to the use of US genetics, particularly when adopted in seasonal pasture-based systems. Several studies related the degree of infertility to the percentage of US Holstein genes in dairy cattle populations (e.g., Grosshans et al., 1997; Wall et al., 2005); it is likely that genetic selection for yield exacerbated the genetic antagonism for reproductive efficiency in dairy cattle.

Reproduction and fertility

Fertility cannot be easily defined as a single trait as it comprises different aspects. First of all, we have to distinguish between female and male fertility. Female fertility has been widely studied, as the loss of reproductive fitness has been primarily assumed to be occurred in cows. Currently, while strong differences in reproductive fitness have been highlighted in cows, few evidences of scarce fertility were detected among bulls at genetic level.

General definitions of fertility have been given. Authors considered it as '*the accomplishment of pregnancy at the desired time*' (Pryce et al., 2004), or '*the ability to produce a living offspring during economically and physiologically approved period*' (Hyppanen and Juga, 1998). It should be noticed that both definitions consider either a physiological and a economical framework. In practice, physiology has to work in the economically imposed terms, and economic return is constrained by the physiology of reproduction.

Female fertility has been defined as '*the ability of the animal to conceive and maintain pregnancy if served at the appropriate time in relation to ovulation*' (Darwash et al., 1997), or '*the ability of the cow to return on heat within an acceptable period, to show the heat in a proper manner, and to become pregnant with a minimum number of inseminations*' (Groen et al., 1997). The framework is substantially more specific here. First, we talk about ovulation. While an healthy and non-lactating cow is not supposed to have any holdback in ovulation (and showing ovulation), lactating dairy cows, especially if high producing, do have problems (Veerkamp et al., 2000; Royal et al., 2002). Energy deficit, imputable to high energy output through milk yield non-compensated by adequate energy input due to limited feed intake, is considered to hamper reproductive performance. Metabolites are shrunk to the mammary gland, and hormones (such as Insulin-like Growth Factors and Insulin) alter glucose availability to the reproductive organs (Veerkamp et al., 2003). Second, the farmer takes the lead. In an artificial insemination (AI) context, assumed the prompt resumption of cyclicity and the showing of recognizable estrous behavior, the decision of inseminating or not the cow is given to the farmer. We generate a case of cow-farmer interaction, and it is recognizable in the time spent till first service after calving, and success at insemination. It should not be neglected that semen quality plays an important role here. Now the cow has to exploit the ability to become (and remain) pregnant with a limited number of inseminations. In addition, cows should have good calving ability and give birth to viable calves (Berglund, 2008). Once that the cow is pregnant is not obvious that the pregnancy will lead to the desired result, as factors reducing cow cycling ability can also obstacle pregnancy maintenance.

As stated above, the success of an insemination is not independent by semen quality. Actually, in advanced AI schemes, semen companies do control semen quality routinely, and discard either batches and bulls not adequate to semen production. Anyway, there are the basis for a concern in a possible role of the service bull (as itself, or due to its genes) in determining success at insemination. Male fertility, the impact of the sire of the embryo in establishing in the uterus of the cow, has been defined as '*the fertilizing ability of the sperm cells and the viability of the embryo*' (Azzam, 1988; Hyppanen and Juga, 1998), or as '*the quality of the sperm cells and the genes transmitted to the embryo*' (Jansen, 1986). We have a complexity of elements in this framework too. While the service sire is imputable for the traits relative to the sperm cells, the genes transmittable to the potential calf influence its survival and viability. Nonetheless, cow's uterus is the environment of potential calf's first months of life, and here female fertility participates as major factor. It often happens that service sire effect is considered as a nuisance variable when estimating the female component of fertility, accounting for the direct genetic effect on embryo establishment and environmental effect on semen quality, which may also vary over time period (Rensing et al., 2006).

Independently by every definition of fertility, it is clear that many factors can affect reproductive performance. We face an interaction of physiology, management practices, and genetic predisposition. Assessment and evaluation of genetic merit for fertility is not trivial, and the complexity of the traits definable leads to the use of appropriate statistical methodologies, which involve non-trivial interpretation of results.

Defining fertility traits

According to the definitions of female fertility reported above, the reproductive fitness of a cow can be expressed in two different categories of traits: interval and success traits (Groen et al., 1997; Weigel, 2004; Andersen-Ranberg et al., 2005). A brief overview of these traits is reported in table 1.

Interval traits measure the distance, usually in days, between two events of relevant importance for reproduction. We define the interval between calving and first heat (**iPH**), interval between calving and start of breeding (as stated specifically by the farmer, called '*voluntary waiting period*', **VWP**), interval between parturition and first service (**iPF**, also known as '*days to first* *service*'), interval between first service and conception (**iFC**), interval between parturition and conception (**iPC**, also known as '*days open*'), and interval between two subsequent parturitions (also known as '*calving interval*', **CI**). Advantages and disadvantages can be highlighted for all the traits. The interval between calving and first heat (iPH) can be considered as the best measure of the ability of the cow to re-cycle after calving (Pryce et al., 2001), but it needs reports of estrous behavior from the farm or measures of endocrine status of cow, and it is not widely used. The interval between parturition and first service (iPF) could be a good assessor of iPH, but VWP plays an important role in differentiating these two traits, as a farmer is not always supposed to inseminate cows at first estrous, or estrous might be not observable for many reasons. The interval between first service and conception (iFC) is an indicator of the time elapsed from the first service to the successful one, and iPC represent a sum of anaestrous period, VWP, and the time taken from the cow to get pregnant. Anyway, iPC needs insemination records to be assessed. When not available, CI can replace it, as a strong genetic correlation binds the two traits (González -Recio et al., 2005a). Unfortunately, CI is restricted only to multiparous cows , as substituting iPC with CI allows the evaluation of the only re-calving cows. Cows which do not calf again are automatically excluded, likely due to fertility problems (Bascom and Young, 1998), therefore overestimating fertility.

Success traits, such as number of inseminations to conception (**INS**), conception at first service (**CFS**), conception rate (**CR**), and non-return indices at a given time (**NR*x***), are the less available and more expensive to collect, and as they require the collection of insemination data, they are more susceptible to biases (König et al., 2008). The number inseminations to conception (INS) measures the number of services needed to achieve pregnancy, and it can be considered a good assessor of fertility, although it does not provide any information about the time elapsed. The conception at first service (CFS) is a simple clustering of INS in 2 classes, as CFS takes value '1' for INS equal to 1, and value '0' for INS greater than 1. The non-return rate at a given time (NR*x*) assumes the insemination to be successful if in a given number of days (*x*) the cow does not return in heat or is not bred again, and expresses the ability of conception and maintaining pregnancy over the period of early gestation (Miglior, 1999). The number of days considered (*x*) is generally comprised between 56 (Jansen, 1986; Hyppanen and Yuga, 1998; Andersen-Ranberg et al., 2003) and 90 (Pasman and Reinhart, 1998; Fuerst and Egger-Danner, 2002; Gredler et al., 2007). Non-return rate at 56 days is also the most widely used trait by Interbull for genetic evaluation of female fertility (Jorjani, 2005; Biffani and Canavesi, 2007). Anyway, considering an *x* number of days in defining the insemination successful may lead to rely on some false positive records. In the elapsed time after each insemination the VWP plays an important role (Andersen-Ranberg et al., 2005; Sun and Su, 2010), and weak estruses may not allow to re-bred, mistaking an established pregnancy with a loss of pregnancy in a weak, infertile and non-re-cycling cow. Therefore the use of an higher number of days to be elapsed has been motivated (Rensing et al., 2006), but a more reliable proof of outcome of a given insemination is provided if the *x* number of elapsed days coincides with pregnancy length. In CR, inseminations are validated as successful according to the estimated pregnancy length they generate (Pasman et al., 2006). This allows to avoid the high number of false positives NR*x* provides, but the necessity of a subsequent calving to validate the insemination leads to a delayed phenotype collection and evaluation.

It is important to consider the several dynamics which underlay fertility traits and the different aspect of fertility they explain. Increase in interval traits is generally linked to decrease in fertility; nonetheless their importance in the herd economy should be considered in relationship with management, since most of interval traits are highly influenced by herd conditions rather than genetic merit (Gallo et al., 2008), and increase in iPC might not be economically adverse if an adequate production level is sustained through longer lactation, also given that the cow might need this to rebuild energy reserves (Dekkers et al., 1998).

Success traits are regarded to have a greater impact on herd economy as elongation of elapsed time before pregnancy achievement can be in part be compensated by lactation length increase (González-Recio et al., 2004), but an additional insemination involves semen dose and veterinary costs, and it cannot be compensated. Furthermore, the same study shows that increasing services needed to achieve pregnancy influence culling risk as well.

The genetic assessment of fertility in the past 60 years

The genetic evaluation of fertility poses some relevant problems. Differently from production traits, which usually follow a normal Gaussian distribution, in fertility traits the same assumptions cannot be considered valid. Interval traits, as the most of time-related measures, generally follow skewed and asymmetric distributions, and success traits are categorical variables, either dichotomous or ordinal. Different treatments of the variables have been proposed, such as log-transformation of skewed distributions (Pollott and Coffey, 2008) or threshold models (Gianola and Sorensen, 1983), although the interpretation of results might be not intuitive when these methods are proposed.

Since threshold-liability models have been postulated and developed (Gianola and Foulley, 1983; Harville and Mee, 1984; Gilmour et al., 1985), this methodology has been widely applied to the analysis of non-linear traits, such as calving difficulty and clinical mastitis, besides fertility. In calving ease, threshold models have been shown to give higher heritability estimates, rank correlation among the sires close to unity (Guerra et al., 2006), and little advantages in predictions (Varona et al., 1999b). In clinical mastitis, Vallimont et al. (2009) and Heringstad et al. (2003) found that threshold models give again higher heritabilities and similar sire ranks to linear models, and Vazquez et al. (2011) reported that predictions between threshold and linear models are comparable. In fertility, no particular improvement has been found in using threshold compared to linear models (Weller and Ron, 1992; Matos et al., 1997).

Similarly, in the last decades animal models have mostly substituted sire models, but their application for non-linear variables is not trivial (Tempelman, 1998), due to long computational times and drawbacks in convergence (Ødegard et al., 2010). The superiority and popularity of animal models have not been widely supported by strong evidences of improvement in prediction of fertility of dairy cows. Sun et al. (2009) found that animal models increased stability and accuracy of genetic evaluation for fertility in dairy cattle, whereas Ramirez-Valverde et al. (2001) did not find any significant improvement in prediction. Moreover, scarce data availability and quality may affect the goodness of assessment. For example, the missing recording of culling reasons or pregnancy check could bias the measure of iPC for a given cow. Data augmentation (Tanner and Wong, 1987; Guo, 2001) has been proposed by several authors as method to overcome this problem, as the direct measure reported is considered as lower bound of a simulated distribution of ‘censored’ records (Chang et al., 2006). Survival analysis has been proposed to be suitable for female fertility evaluation (Weigel, 2004; Gonzàlez-Recio et al., 2006; Hou et al., 2009). Commonly involved measurement is the time elapsed between two reproductive events, mostly parturition, first service and conception.

Heritability of fertility traits. The first step of an investigation at the genetic level is the assessment of the magnitude of genetic variation between individuals. Plenty of studies reported values of heritabilities for the traits reported above, but the vast majority of those were below 0.1. Tables 2, 3, 4, 5, and 6 provide an overview of interval and success traits measured across parities, on first parity only, and on heifers. Different breeds in different countries were used but results did not differ significantly. Results differed mostly according to the methodology used. In general linear models (applied to categorical variables) gave lower heritabilities than threshold models, and animal models gave higher heritability than sire models.

The genetic relationship with production traits. Beside the values of heritability, genetic correlations with milk yield (or the respective selection goal) are also reported in Tables 2, 3, 4, 5, and 6. For heifer fertility, the correlation with first lactation yield is reported. All the estimates show an antagonistic relationship between fertility and production, as already stated above. Magnitude of relationship ranges from null to medium-high values. Heifer fertility is the less correlated to yield, and interval traits are much more related to fertility than success traits. A more detailed discussion of the different values of heritability and correlations will be provided in the specific chapters of the thesis.

Body condition score as a predictor of fertility. The most relevant reason of low fertility is found in lack of energy available for luteal activity (Butler and Smith, 1989). Therefore, a good predictor of fertility has been found in body condition score (BCS). Body condition score provides an assessment of body fat reserves. These reserves become of major importance to keep the regular cycling to go on when milk yield exacerbates energy outputs, and there are reasons to supposed that more conditioned cows will be more fertile.

Bull fertility. The role of male fertility in the dairy industry has often been considered marginal. While female fertility has been widely studied in the last decades, male fertility received less attention. The service sire, i.e., the bull from which semen was collected, plays a role in providing motile spermatozoa and transmitting his genes to the embryo, which will establish or not. Thus, service sires are accounting for their direct genetic effect on embryo establishment and environmental effect on semen quality (Rensing et al., 2006). It often happens that service sire effect is considered as a nuisance variable when estimating the female component of fertility. Within this framework service sires can then be considered unrelated (Weller and Ron, 1992; Weigel and Rekaya, 2000; Jamrozik et al., 2005) or the interaction sire by year of semen production might be of interest (Berry et al., 2010). Otherwise, if the study focused on male fertility, a relationship matrix among the service sire was included, in order to disentangle direct genetic variance from the environmental effect of the service sire (Jansen, 1986; Andersen-Ranberg et al., 2003). Estimates of repeatability and heritability for the direct effect on fertility have often been found to be below (Table 7). Male fertility has often been monitored within breeding companies, which often rely on simple means of non-return or conception rate of bulls, and these evaluations are not always available to farmers. Moreover, the statistical methodology may, in these cases, be sub-optimal, not accounting for confounding effects, such as herd and cow specific factors (Berry et al., 2010).

Possibilities and constraints for selection for fertility in dairy cattle

Selection for fertility is hard, but not impossible. Given the low heritability, and the antagonist genetic correlation with production traits, we expect a slow genetic gain in reproductive efficiency across the generations. However, there are proofs of exploitation of genetic merit for fertility aimed to prevent fertility deterioration in dairy cattle (Andersen-Ranberg et al., 2005). Considering cow's reproductive fitness in the total merit index may allow to stabilize genetic merit for fertility in a cattle population, perhaps to reverse it. The major constraint is data recording, which for reproduction-related events appears to be quite expensive and subject to biases.

Most dairy breeders associations are currently considering genetic merit for fertility in their selection indexes. Norwegian Red breed was the first to introduce non-return rate measured on heifers in 1972 (Heringstad and Larsgard, 2010), and it is now considering several traits in the Joint Nordic Evaluation for fertility together with Sweden, Denmark and Finland (Fogh et al., 2003). Austria and Germany have revised their total merit indexes for Braunvieh and Fleckvieh cattle populations considering now the non-return rate and INS on heifers and cows, and days open, days to first service and CI on cows (Gredler et al., 2007). Canadian Holstein includes fertility and calving ease traits (Miglior, 2007), and US Holstein considers daughters pregnancy rate (Van Raden et al., 2004).

In Italy, the Holstein Breeders Association considers CI, days to first service and non-return rate after first service (Biffani et al., 2006), whereas the Italian Brown Swiss Association considers correlated traits, such as type traits and longevity and BCS (ANARB, 2008).

Table 1: Definition of the most common fertility traits.

Trait	**Acronym**	**Variable**	**Definition**
Interval traits:			
Days from parity to first heat	iPH	Continuous (days)	The days from calving to the first observed heat
Voluntary waiting period	VWP	Continuous (days)	The number of days intentionally left by the farmer before the re-start of breeding
Days from parity to first service	iPF	Continuous (days)	The days from calving to the first service
Days from first service to conception	iFC	Continuous (days)	The days from the first to the successful service (or the last service if no calving is available)
Days from parity to conception	iPC	Continuous (days)	The days from calving to the successful service (or the last service if no calving is available)
Calving interval	CI	Continuous (days)	The number of days between 2 subsequent calvings
Success traits:			
Number of insemination to conception	Ins	Count [1,2…n]	The number of services needed to achieve pregnancy
Conception rate	CR	Binary [0/1]	The outcome of an insemination validated by calving data
Non-return rate at *x* days (x=56-60-70-90)	NR*x*	Binary [0/1]	The outcome of an insemination validated by the occurrence of a second breeding within *n* days

Table 2: Means, heritabilities, and genetic correlations with milk yield[1] for interval fertility traits measured across parities.

Author(s) and Year	Breed (Country)	n° records	Model[2]	Mean	h^2	rg MY
Interval from parturition to first service (iPF)						
Weigel et al., 2000	HO (USA - CA)	~30,000	LAM - REML	70.5	0.058	
Weigel et al., 2000	HO (USA - MN)	~20,000	LAM - REML	91.5	0.061	
Pryce et al., 2001	HO (UK)	1,211	LAM - REML	77.4	0.06	0.49
Berry et al., 2003	HO (IRL)	12,262	LAM - REML	72.8	0.02	-0.08
Kadarmideen et al., 2004	HO (CH)	38,930	LAM - REML	79	0.12	0.27
Biffani et al., 2005	HO (IT)	~250,000	LAM - REML	88	0.06	-0.08
Gonzalez-Recio et al., 2006	HO (E)	71,217	LSM - GS	84	0.05	0.47
L. de Maturana et al., 2007	HO (E)	33,532	rLSM - GS	83.52	0.09	
Konig et al., 2008	HO (D)	73,344 cows	LSM - GS	93.85	0.073	0.14
Interval from parturition to conception (iPC)						
Dematawewa and Berger, 1998	HO (USA)	122,715	LAM - REML	169.3	0.042	0.628
Abdallah and Mc Daniel, 2000	HO (USA)	23,052	LAM - REML	143	0.03	0.62
Pryce et al., 2001	HO (UK)	1,211	LAM - REML	396[3]	0.01	0.74
Dechow et al., 2004	HO (USA)	157,700	LSM - REML		0.04	0.38
Ayagi and Hagiya, 2005	HO (JAP)	483,756	LAM - REML	121.7	0.05	
Biffani et al., 2005	HO (IT)	~250,000	LAM - REML	418[3]	0.07	0.37
Gonzalez-Recio et al., 2006	HO (E)	71,217	LSM - GS	131	0.05	0.63
Gredler et al., 2006	SI (A-D)	3,611	LAM - REML	106.6	0.06	0.74
L. de Maturana et al., 2007	HO (E)	33,532	rLSM - GS	128.64	0.06	
Banos et al., 2009	HO (UK)	593,208	rrLAM - REML	113.5	0.07	0.68

[1] for milk yield is considered the 305 days milk yield on contemporary lactation. [2] LAM = linear animal model; LSM = linear sire model; rLSM = recursive linear sire model; rrLAM = random regression linear animal model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm. [3] Calving interval (CI) was used instead of iPC.

Table 3: Means, heritabilities, and genetic correlations with milk yield[1] for success fertility traits measured across parities.

Author(s) and Year	Breed (Country)	n° records	Model[2]	Days	Mean	h^2	rg MY
Number of inseminations to conception (Ins)							
Dematawewa and Berger, 1998	HO (USA)	122,715	LAM - REML		1.9	0.028	0.436
Berry et al., 2003	HO (IRL)	12,262	LAM - REML		1.8	0.02	0.46
Gonzalez-Recio et al., 2006	HO (E)	71,217	TSM - GS		1.9	0.04	0.23
L. de Maturana et al., 2007	HO (E)	33,532	rTSM - GS		1.89	0.04	
Banos et al., 2009	HO (UK)	593,208	LAM - REML		2	0.05	0.65
Non-return at x days after first service (NR*x*)							
Weigel et al., 2000	HO (USA - CA)	~30,000	LAM - REML	60	0.35	0.014	
Weigel et al., 2000	HO (USA - CA)	~30,000	TAM - REML	60	0.35	0.016	
Weigel et al., 2000	HO (USA - MI)	~20,000	LAM - REML	60	0.57	0.041	
Weigel et al., 2000	HO (USA - MI)	~20,000	TAM - REML	60	0.57	0.034	
Cassel et al., 2003	HO (USA)	73,017	LAM - REML	70	0.52	0.01	
Cassel et al., 2003	JE (USA)	75,357	LAM - REML	70	0.56	0.02	
Kadarmideen et al., 2004	HO (CH)	38,930	LAM - REML	56	0.65	0.06	-0.24
Biffani et al., 2005	HO (IT)	~250,000	LAM - REML	56	0.65	0.03	-0.21
Konig et al., 2008	HO (D)	73,344 cows	TSM - GS	56	0.67	0.029	-0.31
Konig et al., 2008	HO (D)	73,344 cows	TSM - GS	90	0.6	0.028	-0.33
Conception at first service (CFS)							
Pryce et al., 2001	HO (UK)	1,211	LAM - REML		0.46	0.001	
Berry et al., 2003	HO (IRL)	12,262	LAM - REML		0.49	0.01	-0.29
L. de Maturana et al., 2007	HO (E)	33,532	rTSM - GS		0.51	0.12	

[1]for milk yield is considered the 305 days milk yield on contemporary lactation. [2]LAM = linear animal model; TAM = threshold animal model; TSM = threshold sire model; rTSM = recursive threshold sire model; REML = restricted maximum likelihood algorithm;

Table 4: Means, heritabilities, and genetic correlations with milk yield[1] for interval from parturition to first service (**iPF**) measured on first lactation.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Mean**	**h^2**	**rg MY**
Berger et a., 1981	HO (USA-CA)	72,187	LSM - Hend. III	85	0.04	0.48
Hansen et al., 1983	HO (USA)	41,710	LSM - Hend. III		0.03	
Hermas et al., 1987	GUE (USA)	741	LSM - Hend. III		0.13	0.11
Mantysaari and van Vleck, 1989	AYR (SF)	~60,000	LAM - REML	81	0.13-0.23	0.31-0.15
Weller	HO (IL)	91,770	LSM - Hend. III		0.048	0.271
Grosshans et al., 1997	HO (NZ)	26,393	LSM - REML	86.6	0.03	0.25
Grosshans et al., 1997	JE (NZ)	14,345	LSM - REML	81.7	0.03	0.25
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	89	0.07	0.53
Rossoni et al., 2002	BS (IT)	73,125	LAM - REML	83.66	0.11	
Haile-Mariam et al., 2003	HO (AUS)	~17,000	LSM - REML	77	0.13	
Wall et al., 2003	HO (UK)	~30,000	LSM - REML	81.61	0.035	0.49
Andersen-R. et al., 2005	NR (NOR)	>200,000	LSM - REML	81	0.020-0.025	0.47
Mitchell et al., 1989	HO (USA)	~6,000	LAM - REML	85.8	0.04	
Gredler et al., 2007	SI (A-D)	38,498	LAM - REML	70.9	0.06	
Estrada-Leon et al., 2008	BS (MEX)	~1,000	LAM - REML	87.8	0.04	
Holtsmark et al., 2008	NR (NOR)	~524,268	LSM - GS		0.03	0.48
Liu et al., 2008	HO (D)	282,183	LAM - REML		0.039	0.34
Heringstad et al., 2009	NR (NOR)	55,568	rLSM - GS	77.4	0.04	
Hou et al., 2009	HO (DK)	475,926	LAM- GS	81-198	0.102	
Hou et al., 2009	HO (DK)	475,926	cLSM - GS	81-198	0.108	
Hou et al., 2009	HO (DK)	475,926	cLSM - GS	81-198	0.106	
Hou et al., 2009	HO (DK)	475,926	SURV	81-198	0.213	
Hou et al., 2009	HO (DK)	475,926	SURV	81-198	0.0125	
Sun et al., 2009	HO (DK)	471,742	LAM - REML	81.27	0.081	
Buch et al., 2010	SR (S)	~500,000	LAM - REML	87	0.038	0.3

[1]for milk yield is considered the 305 days milk yield on first lactation. [2]LAM = linear animal model; rLSM = recursive linear sire model; cLSM = censored linear sire model; Hend. III = Henderson method 3; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm.

Table 5: Means, heritabilities, and genetic correlations with milk yield[1] for interval from parturition to conception (**iPC**) measured on first lactation.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Mean**	**h^2**	**rg MY**
Berger et a., 1981	HO (USA-CA)	72,187	LSM - Hend. III	135	0.02	0.62
Hansen et al., 1983	HO (USA)	41,710	LSM - Hend. III	.	0.03	
Jansen, 1986	HO (NL)	12,708	LSM - REML	96.6	0.015	
Hermas et al., 1987	GUE (USA)	741	LSM - Hend. III		0.04	0.74
Hoeschele, 1990	HO (USA)	379,009	LSM - REML	.	0.027	
Campos et al., 1994	HO (USA-FL)	~4,000	LAM - REML	166	0.052	0.159
Campos et al., 1994	JE (USA-FL)	~2,000	LAM - REML	127	0.026	0.268
Grosshans et al., 1997	HO (NZ)	26,393	LSM - REML	101.1	0.02	0.25
Grosshans et al., 1997	JE (NZ)	14,345	LSM - REML	96.4	0.02	0.25
Dematawewa and Berger, 1998	HO (USA)		LAM - REML		0.12	0.55
Pryce et al., 2000	HO (UK)	19,042	LAM - REML	385 CI	0.022	
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	127	0.066	0.61
Haile-Mariam et al., 2003	HO (AUS)	~17,000	LSM - REML	372 CI	0.04	
Lee et al., 2003	HO (Korea)	11,472	LAM - REML	113.4	0.024	-0.279
Wall et al., 2003	HO (UK)	~30,000	LSM - REML	387.64	0.033	0.27
Muir et al., 2004	HO (CDN)	33,312	LAM - GS	395.41 CI	0.07	0.51
Mitchell et al., 1989	HO (USA)	~6,000	LAM - REML	140.3	0.05	
Chang et al., 2006	NR (NOR)	1,454,916	LSM - GS	68-200	0.04	
Dal Zotto et al., 2007	BS (IT)	32,359	LAM - REML	421.0 CI	0.05	0.56
Gredler et al., 2007	SI (A-D)	38,498	LAM - REML	105.6	0.04	
Estrada-Leon et al., 2008	BS (MEX)	~1,000	LAM - REML	172.8	0.05	
Liu et al., 2008	HO (D)	282,183	LAM - REML		0.026	0.41
Hou et al., 2009	HO (DK)	475,926	LAM- GS	120-208	0.066	
Hou et al., 2009	HO (DK)	475,926	cLSM - GS	120-208	0.069	
Hou et al., 2009	HO (DK)	475,926	cLSM - GS	120-208	0.068	
Hou et al., 2009	HO (DK)	475,926	SURV	120-208	0.121	
Hou et al., 2009	HO (DK)	475,926	SURV	120-208	0.0088	
Sun et al., 2009	HO (DK)	471,742	LAM - REML	133.29	0.067	

[1] for milk yield is considered the 305 days milk yield on first lactation. [2] LAM = linear animal model; rLSM = recursive linear sire model; cLSM = censored linear sire model; Hend. III = Henderson method 3; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm.

Table 6: Means, heritabilities, and genetic correlations with milk yield[1] for number of inseminations to conception (**INS**) measured on first lactation.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Mean**	**h^2**	**rg MY**
Berger et al., 1981	HO (USA - CA)	72,187	LSM - Hend. III	2.1	0.01	0.62
Hansen et al., 1983	HO (USA)	41,710	LSM - Hend. III		0.02	
Hermas et al., 1987	GUE (USA)	741	LSM - Hend. III		0.01	0.31
Raheja et al., 1989	HO (CDN)	53,705	LSM - REML	1.38	0.04	0.01
Oltenacu et al., 1991	SRW (S)	48,830	LSM - EM	1.87	0.05	0.09
Oltenacu et al., 1991	SBW (S)	21,136	LSM - EM	1.7	0.05	0.09
Grosshans et al., 1997	HO (NZ)	26,393	LSM - REML	1.49	0.01	0.17
Grosshans et al., 1997	JE (NZ)	14,345	LSM - REML	1.51	0.01	0.17
Dematawewa and Berger, 1998	HO (USA)		LAM - REML		0.03	0.53
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	2	0.034	0.48
Haile-Mariam et al., 2003	HO (AUS)	~17,000	LSM - REML	1.85	0.03	
Wall et al., 2003	HO (UK)	~30,000	LSM - REML	1.67	0.02	0.06
Jamrozik et al., 2005	HO (CDN)	53,158	LAM - GS	1.64	0.029	
Chang et al., 2006	NR (N)	1,454,916	cLAM - GS		0.04	
Gredler et al., 2007	SI (A-D)	38,498	LAM - REML	1.84	0.022	
Estrada-Leon et al., 2008	BS (MEX)	~1,000	LAM - REML	2.41	0.04	
Sun et al., 2010	HO (DK)	471,742	LAM - REML	2.244	0.028	
Buch et al., 2010	SR (S)	~500,000	LAM -REML	1.8	0.018	0.47

[1]for milk yield is considered the 305 days milk yield on first lactation. [2]: LAM = linear animal model; TSM = threshold sire model; TAM = threshold animal model; rTSM = recursive threshold sire model; rrTAM = random regression threshold animal model; cLAM = censored linear animal model; Hend. III = Henderson method 3; EM – expectation maximization algorithm; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm;

Table 7: Means, heritabilities, and genetic correlations with milk yield[1] for conception rate (**CR**) measured on first lactation.

Author(s) and Year	Breed (Country)	n° records	Model[2]	Mean	h^2	rg MY
Jansen, 1986	HO (NL)	12,708	LSM - REML	0.694	0.013	
Hermas et al., 1987	GUE (USA)	741	LSM - Hend. III		0.03	-0.2
Oltenacu et al., 1991	SR (S)	48,830	LSM - EM	0.5	0.05	-0.07
Oltenacu et al., 1991	SB (S)	21,136	LSM - EM	0.57	0.05	-0.08
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	0.27	0.016	-0.49
Haile-Mariam et al., 2003	HO (AUS)	~17,000	LSM - REML	0.47	0.02	
Averill et al., 2004	HO (USA)	297,823	TAM - GS	0.43	0.028	
Mitchell et al., 2005	HO (USA)	~6,000	LAM - REML	0.273	0.01	
Averill et al., 2006	HO (USA)	369,353	rrTAM - GS		0.03-0.11	
Sun et al., 2010	HO (DK)	471,742	LAM - REML	0.416	0.017	
Sun et al., 2010	HO (DK)	471,742	Logit	0.416	0.048	
Sun et al., 2010	HO (DK)	471,742	Probit	0.416	0.019	

[1]for milk yield is considered the 305 days milk yield on first lactation. [2]: LAM = linear animal model; TSM = threshold sire model; TAM = threshold animal model; rTSM = recursive threshold sire model; rrTAM = random regression threshold animal model; cLAM = censored linear animal model; Hend. III = Henderson method 3; EM – expectation maximization algorithm; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm;

Table 8: Means, heritabilities, and genetic correlations with milk yield[1] for non-return rate measured on first lactation.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Days**	**Mean**	**h^2**	**rg MY**
Jansen, 1986	HO (NL)	12,708	LSM - REML	56	0.745	0.028	
Mantysaari and Van Vleck, 1989	AYR (SF)	~60,000	LAM - REML	120	0.49	0.02	0.06
Hodel et al., 1995	SI (CH)	706,040	LSM - REML	90	0.611	0.021	
Grosshans et al., 1997	HO (NZ)	26,393	LSM - REML	42	0.727	0.03	-0.19
Grosshans et al., 1997	JE (NZ)	14,345	LSM - REML	42	0.774	0.03	-0.19
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	56	0.49	0.019	-0.41
Wall et al., 2003	HO (UK)	~30,000	LSM - REML	56	0.65	0.018	-0.25
Muir et al., 2004	HO (CDN)	33,312	LAM - GS	56	0.6441	0.04	0.02
Andersen-R. et al., 2005	NR (N)	~200,000	TSM - GS	56	0.67	0.036	-0.18
Andersen-R. et al., 2005	NR (N)	~200,000	LSM - REML	56	0.67	0.012	
Jamroziket al., 2005	HO (CDN)	53,158	LAM - GS	56	0.74		
Heringstad et al., 2006	NR (N)	475,270	TSM - GS	56	0.68	0.02	
Gredler et al., 2007	SI (A-D)	38,498	LAM - REML	56	0.666	0.011	
Holtsmark et al., 2008	NR (N)	~524,268	TSM - GS	56	0.67	0.02	-0.24
Liu et al., 2008	HO (D)	282,183	LAM - REML	56		0.015	-0.2
Heringstad et al., 2009	NR (N)	55,568	rTSM - GS	56	0.67	0.06	
Sun et al., 2010	HO (DK)	471,742	LAM - REML	56	0.563	0.012	
Sun et al., 2010	HO (DK)	471,742	LAM - REML	56	0.563	0.011	
Sun et al., 2010	HO (DK)	471,742	Logit	56	0.563	0.034	
Sun et al., 2010	HO (DK)	471,742	Probit	56	0.563	0.014	

[1]for milk yield is considered the 305 days milk yield on first lactation. [2]: LAM = linear animal model; TSM = threshold sire model; TAM = threshold animal model; rTSM = recursive threshold sire model; rrTAM = random regression threshold animal model; cLAM = censored linear animal model; Hend. III = Henderson method 3; EM – expectation maximization algorithm; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm;

Table 9: Means, heritabilities, and genetic correlations with milk yield[1] for conception rate (**CR**) measured on first lactation.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Mean**	**h^2**	**rg MY**
Jansen, 1986	HO (NL)	12,708	LSM - REML	0.694	0.013	
Hermas et al., 1987	GUE (USA)	741	LSM - Hend. III		0.03	-0.2
Oltenacu et al., 1991	SRW (S)	48,830	LSM - EM	0.5	0.05	-0.07
Oltenacu et al., 1991	SBW (S)	21,136	LSM - EM	0.57	0.05	-0.08
Veerkamp et al., 2001	HO (NL)	177,220	LSM - REML	0.27	0.016	-0.49
Haile-Mariam et al., 2003	HO (AUS)	~17,000	LSM - REML	0.47	0.02	
Averill et al., 2004	HO (USA)	297,823	TAM - GS	0.43	0.028	
Mitchell et al., 2005	HO (USA)	~6,000	LAM - REML	0.273	0.01	
Averill et al., 2006	HO (USA)	369,353	rrTAM - GS		0.03-0.11	
Sun et al., 2010	HO (DK)	471,742	LAM - REML	0.416	0.017	
Sun et al., 2010	HO (DK)	471,742	Logit	0.416	0.048	
Sun et al., 2010	HO (DK)	471,742	Probit	0.416	0.019	

[1] for milk yield is considered the 305 days milk yield on first lactation. [2]: LAM = linear animal model; TSM = threshold sire model; TAM = threshold animal model; rTSM = recursive threshold sire model; rrTAM = random regression threshold animal model; cLAM = censored linear animal model; Hend. III = Henderson method 3; EM – expectation maximization algorithm; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm;

Table 10: Means, heritabilities, and genetic correlations with milk yield[1] for success fertility traits measured on heifers.

Author(s) and Year	**Breed (Country)**	**n° records**	**Model[2]**	**Days**	**Mean**	**h^2**	**rg MY**
Number of inseminations to conception (Ins)							
Hansen et al., 1983	HO (USA)	41,710	LSM - Hend. III		1.7	0.03	
Oltenacu et al., 1991	SRW (S)	48,830	LSM - EM		1.53	0.05	0.13
Oltenacu et al., 1991	SBW (S)	21,136	LSM - EM		1.44	0.04	0.13
Gredler et al., 2003	SI (A-D)	22,865	LAM - REML		1.52	0.021	
Non-return at x days after first service (NR*x*)							
Jansen, 1986	HO (NL)	8,972	LSM - REML	56	0.768	0.007	
Mantysaari and Van Vleck, 1989	AYR (SF)	~60,000	LAM - REML	120	0.62	0.02-0.03	0.03-0.14
Hodel et al., 1995	SI(CH)	345,775	LSM - REML	90	0.732	0.011	
Andersen-R. et al., 2003	NR (N)	1,632,961	LSM - REML	56	0.75	0.012-0.014	0.04
Gredler et al., 2003	SI (A-D)	22,865	LAM - REML	56	0.778	0.013	
Muir et al., 2004	HO (CDN)	33,312	LAM - GS	56	0.7829	0.03	0.12
Holtsmark et al., 2008	R (N)	649,156	TSM - GS	56	0.75	0.02	-0.07
Liu et al., 2008	HO (D)	215,509	LAM - REML	56		0.012	-0.11
Conception at first service (CFS)							
Jansen, 1986	HO (NL)	8,972	LSM - REML		0.731	0.013	
Oltenacu et al., 1991	SRW (S)	48,830	LSM - EM		0.65	0.04	-0.12
Oltenacu et al., 1991	SBW (S)	21,136	LSM - EM		0.7	0.06	-0.13

[1]for milk yield is considered the 305 days milk yield on first lactation. [2]: LAM = linear animal model; TSM = threshold sire model; Hend. III = Henderson method 3; EM – expectation maximization algorithm; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

Tabella 11: Means, heritabilities (h^2), and repeatabilities (r) estimated for the service sire effect on non-return at 56 days (NR56) and conception rate (CR).

Author(s) and year	**Breed (Country)**	**n° records**	**Model**[1]	**NR56**			**CR**		
				Mean	**h^2**	**r**	**Mean**	**h^2**	**r**
Taylor *et al.* 1985	HO (USA)	329,314 (882)	LSM				0.6	0.06	0.06
Jansen, 1986	HO (NL)	28,977	LSM - REML	0.77	0.021		0.73	0.024	
		23,907		0.75	0.009		0.7	0.013	
		18,517		0.72	0.014		0.68	0.015	
Nadarajah *et al. 1988*	HO (CDN)	298,013 (746)	Sire-Son-Reg				0.59	0.158	
Weller and Ron, 1992	HO (ISR)	131,486	TSM - REML						0.0037
Hyppanen and Juga, 1998	AYR (SF)	154,066	LSM - REML	0.64	0.001				
Weigel and Rekaya, 2000	HO (USA-CA)	29,215 (1,231)	LAM – REML	0.35		0.005	0.41		0.002
			TAM – REML			0.007			0.004
	Ho (USA-MN)	19,203 (1,079)	LAM – REML	0.57		0.003	0.46		0.004
			TAM – REML			0.005			0.006
Andersen-Ramberg *et al.*, 2003	NR (NOR)	1,632,961	LSM - REML	0.75	0.01				
Weigel , 2004	HO (USA)	515,915	TAM					0.003	0.003
Jamrozik *et al.*, *2005*	HO (CDN)	53,158	LAM - GS	0.74		0.2			
Averill *et al.*, 2006	HO (USA)	369,353	rrTM - GS				0.57		0.0101
Kuhn and Hutchinson, 2008	HO (USA)	40,953	LAM					0.0002	
			TSM					0.00013	
Berry *et al.*, 2010	HO (IRL)	361,412	LAM_REML					0.001	0.009

[1]: LAM = linear animal model; LSM = linear sire model; TSM = threshold sire model; TAM = threshold animal model; rrTM = random regression threshold model; cLAM = censored linear animal model; Sire-Son-Reg = Sire Son Regression; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm;

Aims of the thesis

The aims of these thesis are to provide a genetic assessment for reproductive efficiency in dairy cattle. The population of Italian Brown Swiss reared in the province of Bolzano (South Tyrol) suits for this purpose. Here, an efficient recording scheme allows full storage of inseminations records. These records will be organized in database, where the fertility measures are reported. The study will be conducted following two major lines: female fertility and male fertility.

For the female fertility investigation, the commonly used interval and fertility traits will be considered. Here, in a first step, an overall genetic analysis is to be conducted in order to quantify the magnitude of resemblance among individuals on the genetic level, i.e. to calculate genetic parameters for fertility traits. These fertility traits will be also considered for their relationship with productive traits, which have been the most relevant breeding goal in the vast majority of dairy cattle breeds, Italian Brown Swiss included. By the way, the feasibility and reliability of considering interval traits in a ‘more biological’ manner will be considered.

The second step, will consist of deepening genetic analysis within parity orders, i.e. first parity fertility is supposed to be a different trait to second parity fertility, etc. Actually, is not the trend of reproductive fitness to be of interest, but the variance and covariance structure underlying reproductive performance across parities. As fertility, lactating cows will be compared to heifers, but the latter will be also compared to the former’s yield.

It’s almost unconceivable to measured reproductive efficiency punctually. Therefore candidate traits, such as body condition score, may play an important role in this. The third and last step of female fertility investigation will concern its association with the cow’s condition scoring.
Condition, assessed once on first lactation in Italian Brown Swiss, will be related to contemporary fertility measures, contemporary yield, and subsequent fertility.

For the sake of completeness, the bull’s role in determining the success of reproductive events cannot be neglected. Bulls, service sires actually, will be evaluated for their relative success to a performed artificial insemination. There’s no concern nowadays for the genetic selection of the most fertile bull. Selection for semen quality and efficiency is done phenotypically, thus the male fertility investigation will be addressed to prediction of bull semen fertility, on a genetic basis. Different models with different assumptions will be considered, the comparison will be made through specific statistics bearing the binary nature of the trait.

Chapter two

Prediction of dairy bull fertility from field data: comparison of models in Italian Brown Swiss.

Introduction

Considering the possible causes of loss in reproductive fitness in dairy cattle, female fertility has been widely studied in the last decades, while male fertility received less attention. Possible reasons of low reproductive performance have therefore been found either in cow metabolism, where the shrunk of energies to the mammary gland would have hampered correct reproductive function (Veerkamp et al., 2003), and in an antagonistic effect of pleyotropic genes affecting milk yield and fertility (Royal et al., 2000; Lucy, 2001, Pryce et al., 2001). Anyway, there are the basis for a concern about the impact of male fertility in the dairy industry efficiency (Nadarajah et al., 1988; Clay and McDaniel, 2004; Blaschek et al., 2011).

From a male fertility viewpoint, it’s the fertilizing ability of the service sire sperm cells and the viability of the embryo to be of interest (Azzam, 1988; Hyppanen and Juga, 1998, Jansen, 1986). The many factors affecting these traits should be distinguished in an heritable fraction (variation due to the genes transmitted), and a variation peculiar of the individual which is not explainable by an additive genetic effect. The latter, could be further distinguished in what is ‘permanent’ in the service sire (e.g. consanguinity) or ‘temporary’, thus varying over time periods (effect a certain batch of semen doses within the service sire). Whatever, in bull fertility, the additive genetic effect is mostly recognizable in the genes transmitted to the embryo and affecting its establishment (Jansen, 1986), while both permanent and temporary effects can be considered ‘environmental’, and imputable to service sire semen quality (Rensing et al., 2006).

Service sires are often compared in terms of success to a performed artificial insemination, not differently by female fertility. The most common trait used is non-return at 56 days after insemination (NR*x*), or conception rate (CR). As the 2 traits are computed differently, a comparison between them might better comprehend fertility assessment (Sun and Sun, 2010).

Among the factors affecting male fertility, those non-genetic can be summarized as year and period of the year of insemination (Taylor et al., 1985; Andersen-Ramberg et al., 2003), bred cow (Clay and McDaniel, 2004; Berry et al., 2010), parity and stage of lactation of the bred cow (Fuerst and Egger-Danner, 2002; Kuhn and Hutchinson, 2008), herd (Jansen, 1986; Hyppanen and Juga, 1998) or herd-year interaction (Andersen-Ramberg et al., 2003; Berry et al., 2010), and technician performing the insemination (Jansen and Lagerweij, 1987; Hyppanen and Juga, 1998). Moreover, a possible effect of age of the bull on its fertilizing ability has been found, but it’s mostly imputable to a non-random mating to the cows (Taylor et al, 1985; Kuhn and Hutchinson, 2008), respective to the genetic merit for milk yield of the cow itself. As this trend over service sire’s lifetime might be not linear, some authors proposed the use of classes, where bulls should be compared primarily between undergoing progeny test and proven (Peddinti et al., 2008), and secondarily between different ages within being tested (Rensing et al., 2006).

In studies focusing on male fertility, Values for repeatability (Weigel and Rekaya, 2000; Jamrozik et al., 2005; Berry et al., 2010) and heritability (Andersen-Ranberg et al. 2003; Hyppanen and Juga; 1998; Kuhn and Hutchinson; 2008) for the direct effect on fertility have often been found to be below 0.02. The most likely reason has been found in the difficult of accounting for all the effects influencing fertility which cannot be disentangled in routinary collection of fertility field data, as laboratory semen parameters appear to be more heritable, although not really related to field fertility (Ducrocq and Humblot, 1995; Mathevon et al., 1998; Gredler et al., 2007).

Besides variance components for bull fertility, also predictions on a genetic basis may play an important role. The most used and reliable tool for the assessment of model predictive ability is cross validation, which has already been exploited in dairy cattle (Caraviello et al., 2004; Gonzalez-recio et al., 2005; Vazquez et al., 2011) and other species (Matos et al., 1997; Cecchinato et al, 2010). For bull fertility it has been investigated by Kuhn and Hutchinson (2008) and Blaschek et al. (2011), with different approaches. Unfortunately, given the low heritability and repeatability of male fertility nowadays found, it is expected that the correlation between predicted and true breeding value for this trait be low.

The aim of this study was therefore to investigate the role of service sire in fertility of dairy cattle comparing different traits(conception rate *vs.* non return rate), pedigree individuals (sire *vs.* animal models), distribution assumptions (linear *vs.* threshold models) and specifications in terms of random effects . This comparison will be performed either in terms of genetic parameters, goodness of fit, and predictive ability of different models..

Materials and Methods

Data

Service and production records on Brown Swiss cows were obtained from the Breeders Association of Bolzano-Bozen province (Italy), a similar dataset was already used in a study on female's fertility (Tiezzi et al., 2011). A dataset containing more than 200,000 single insemination records performed on Brown Swiss cows and heifers between 1999 and 2008 was constructed. Inseminations were validated as successful for conception rate (CR) when giving an acceptable pregnancy length of 288±15 days (mean value from Norman et al., 2009). If two inseminations resulted successful within this range of pregnancy length the latter was considered successful. If pregnancy length was lower than 273 the cow was not validated as pregnant, and every cow having records in a given lactation was required to have a successful insemination on the previous lactation. Non-return at 56 days (NR) was also calculated for every service, validated as non-returned if no inseminations were performed within 56 days. From the whole dataset we extracted only those inseminations performed with registered AI Brown Swiss bulls as service sire. Service sires were required to have at least 100 observations, herds and technicians were required to have at least 20 observations. Furthermore sires of cows with less than 20 observations and cows with less than 2 observations were not considered. Leniency in the editing of sires of the cows stemmed from the fact that female fertility was considered here just a nuisance variable. Levels, for service sires, herds, technicians and sires of cows, were considered if showing a mean for CR and NR bounded between 0.1 and 0.9. Although interactions between effects were not fitted (e.g. technician*service sire) those levels showing only one corresponding level for the other effect were edited. For example, a technician was requested to operate in more than one farm, and in each farm more than a single technician was requested to be found. This was done for all the effects fitted (except cow by sire of cow). After editing, 124,206 single insemination records were available for analyses in the main dataset ($\mathrm{DATA_{TOT}}$).

Statistical analysis and models involved

Models involved in the analysis were linear-sire, threshold-sire, linear-animal and threshold animal models.

Sire and animal models- For constructing sire and animal models, different pedigree files were edited. For sire models, a sire-MGS pedigree was considered, tracing back generations starting up with service sires and sires of cows as animals with phenotype, while for animal models the embryo resulting from every service sire-cow mating was coded and appended to animals (sires and dams) in pedigree.

Linear and threshold models- Although the assumptions of a linear model are violated for the traits analyzed, linear mixed models were run to be compared with threshold models, supposed to be more appropriate (Gianola, 1982) and with most of the results in the literature. For the threshold models, a single threshold is considered in the analysis, and an underlying variable called liability is generated from data, according to the following assumption:

$$yi = \begin{cases} 0\; if \;\; \lambda \leq \tau \\ 1\; if \;\; \lambda > \tau \end{cases}$$

Where y_i is the i^{th} observation (0/1), $\boldsymbol{\lambda}$ is the liability, $\boldsymbol{\tau}$ is the given threshold. In accordance to the formula, every observation y_i takes value 1 (success for CR or NR) if the liability overcomes the value $\boldsymbol{\tau}$, is 0 (failure in CR or NR) otherwise. The liability is assumed to follow a normal distribution with mean μ and variance $I\sigma^2_e$. As $\boldsymbol{\tau}$ and σ^2_e are not identifiable and to simplify computation, σ^2_e is fixed to '1' and $\boldsymbol{\tau}$ is fixed to '0', thus no sampling of the threshold value is needed.

Model specifications- Within the comparison reported above, four different model structures increasing in complexity were considered. Animal permanent environmental and genetic effects were added sequentially:

Model A: $\mathbf{y(\lambda)} = \mathbf{X\beta} + \mathbf{Z_{he}he} + \mathbf{Z_{te}tc} + \mathbf{Z_{dg}dg} + \mathbf{e}$,

Model B: $\mathbf{y(\lambda)} = \mathbf{X\beta} + \mathbf{Z_{he}he} + \mathbf{Z_{te}tc} + \mathbf{Z_{dg}dg} + \mathbf{Z_{me}me} + \mathbf{e}$,

Model C: $\mathbf{y(\lambda)} = \mathbf{X\beta} + \mathbf{Z_{he}he} + \mathbf{Z_{te}tc} + \mathbf{Z_{dg}dg} + \mathbf{Z_{me}me} + \mathbf{Z_{mg}mg} + \mathbf{e}$,

Model D: $\mathbf{y(\lambda)} = \mathbf{X\beta} + \mathbf{Z_{he}he} + \mathbf{Z_{te}tc} + \mathbf{Z_{dg}dg} + \mathbf{Z_{me}me} + \mathbf{Z_{mg}mg} + \mathbf{Z_{de}de} + \mathbf{e}$,

Where **y** are the binary observations (0/1) for linear models, **λ** is the unobserved liability for threshold models, **β** is the vector of fixed effect, **he** is the vector of herd effects, **tc** is the vector of technician effect, **dg** is the vector of direct genetic effect, **me** is the vector of maternal environmental effect, **mg** is the vector of maternal genetic effect, **de** is the vector of direct environmental effect, **e** is the vector of residuals. $\mathbf{X}$, $\mathbf{Z_{he}}$, $\mathbf{Z_{tc}}$, $\mathbf{Z_{dg}}$, $\mathbf{Z_{me}}$, $\mathbf{Z_{mg}}$ and $\mathbf{Z_{de}}$ are the relative incidence matrices of the appropriate order.

All models accounted for the "fixed" effects of year_season of insemination (40 levels), class of parity*dim at insemination (age at insemination for heifers); status of the service sire at insemination (progeny testing/proven), and the random effects of herd [assumed with mean 0 and variance $\mathbf{I\sigma^2}_e$], technician [$\mathbf{te} \sim N(0, \mathbf{I\sigma^2}_{te})$], and residual error [$\mathbf{e} \sim N(0, \mathbf{I\sigma^2}_e)$].

Model A includes direct genetic effect, accounted by a service sire effect in sire models and an embryo effect on animal models. Both were assumed normally distributed with mean **0** and variance $\mathbf{A\sigma^2_{dg}}$, where A is the appropriate relationship matrix. Model B is similar model A with the inclusion of maternal environmental effect in order to account for a non-random mating of bulls to cows. Cows are assumed being with mean 0, normally distributed and unrelated among them [$\mathbf{me} \sim N(0, \mathbf{I\sigma^2}_{me})$], In model C the maternal genetic effect is added represented by sires of cows in sire models and cows in animal models. These are assumed related among them [$\mathbf{mg} \sim N(0, \mathbf{A\sigma^2}_{mg})$], with the appropriate relationship matrix. Here direct-maternal covariance is estimated. In model D the direct environmental effect of the service sire is added beside the additive genetic effect. Service sires are considered unrelated here [**de** ~ $N(0, \mathbf{I}\boldsymbol{\sigma}^2_{de})$].

The different models were run in a Bayesian framework via Gibbs sampling algorithm, in order to obtain variance components. Flat priors were assumed for all ‘fixed’ effects, while for the random effects the specific prior assumptions of distributions are reported above. Sire solution estimates were obtained solving the BLUP equation with the mean value of the posterior distribution of the respective variance components obtained. For all the computations the software TM by Legarra et al. (2008) was used. For all models 550,000 iterations were run with the first 50,000 discarded as burn-in. Thinning occurred every 50 iterations, storing 10,000 samples from every computation for inferences. Convergence was assessed by visual inspection of trace plots.

Heritability (h^2) was computed as follows for sire and animal models, respectively:

$$h^2(sire) = \frac{4\sigma^2_{dg}}{\sigma^2_{dg} + \sigma^2_{de} + \sigma^2_{me} + \sigma^2_{mg} + \sigma_{dg-mg} + \sigma^2_{he} + \sigma^2_{te} + \sigma^2_{e}}$$

$$h^2(animal) = \frac{\sigma^2_{dg}}{\sigma^2_{dg} + \sigma^2_{de} + \sigma^2_{me} + \sigma^2_{mg} + \sigma_{dg-mg} + \sigma^2_{he} + \sigma^2_{te} + \sigma^2_{e}}$$

Where σ^2_{dg}, σ^2_{de}, σ^2_{me}, σ^2_{mg}, σ^2_{he} , σ^2_{te} are the variance components descripted above, σ_{dg-mg} is the service sire-sire of cow covariance in sire models and embryo-cow covariance in animal models. Variance and covariances reported in formulas were omitted from the denominator when not estimated (Models A, B, C). Means, lower and upper bounds of the 95% highest posterior probability density regions for heritabilities were estimated from the Gibbs samples.

Model comparison

Validation study. Disassembly of dataset was made according to a year-split approach criterion. The calibration dataset ($DATA_{05}$) started at year 1999 and was truncated at year 2005. Validation dataset ($DATA_{08}$) contained years 2006-2008. Variance components were calculated both for $DATA_{TOT}$ and $DATA_{05}$. EBVs were obtained solving the BLUP equation with the respective dataset and variance components from models A, B, C and D. In addition, from model D also EBVs for D+ were calculated, as the sum of additive genetic and environmental solutions for the service sire. $DATA_{TOT}$ generated EBV_{TOT} and $DATA_{05}$ generated EBV_{05}.

Two different predictions were performed in order to compare models. First, service sires excluded from $DATA_{05}$ were estimated through relationship matrix with each model, and their pedigree EBV_{05} was compared with their average CR and NR in $DATA_{08}$ (CR_{08} and NR_{08}, respectively). This was called 'prediction of the young bulls'. In a second time, only service sires showing at least 70 observations in $DATA_{05}$ and 30 observations in $DATA_{08}$ were considered, and their EBV_{05} was compared with CR_{08} and NR_{08}. in order to predict a possible evolution of service sire fertility starting from fewer observations, calling this method 'prediction of proven bulls'.

Goodness of fit was assessed using the local weighted regression (Cleveland and Loader, 1996) between the EBV_{TOT} obtained with each model (A, B, C, D, D+) and the phenotypic mean of the outcomes of every service sire in $DATA_{TOT}$. The PROC LOESS procedure is SAS version 9.2.1 was used for fitting, this was set in order to choose the best smoothing parameter from each model according to the AIC. Models were compared in terms of mean squared error (**MSE**) obtained.

Predictive ability for each model was assessed via sum of χ^2 (Caraviello et al., 2004; Gonzalez-recio et al., 2005; Cecchinato et al., 2010). Binary indicators of success in $DATA_{08}$ were regressed (using logistic regression) on EBV_{05} obtained from each model such that the EBV_{05} could be converted into the service sire probability of conception for both traits. These were multiplied by the number of observations respective to every service sire in $DATA_{08}$ in order to obtain an expected number of success and failures. χ^2 was calculated for every service sire between the expected success and failures deriving from each EBV_{05} and the observed success and failures in $DATA_{08}$.

$$\chi^2 = [(\text{expected success-observed success})^2 + (\text{expected failures-observed failures})^2]$$

χ^2 values were summed across sires such that each model generated a single sum of χ^2 used for model comparison.

Results and Discussion

Data

In table 1 are reported the descriptive statistics for the dataset used. The final dataset ($DATA_{TOT}$) consisted of 124,206 records. These were distributed over 40 classes of year-season of breeding, 26 classes of parity*days in milk of the cow, 2 classes of status of the bull at service. Inseminations were performed in 1,400 herds by 86 technicians, on 28,873 cows sired by 513 sires. Service sires were 306 and averaged 406 insemination each, ranging from 100 to 8,255. The pedigree file included 1,292 individuals in the sire-MGS model, 176,829 in the animal model. The overall mean for CR was 0.48 while was 0.70 for NR. Standard deviations were 0.50 and 0.46, respectively. It is to be noticed that 23% of data were discordant, giving success for NR and failure for CR. NR appears to be a moderate indicator of fertility if we assume CR to be the one reflecting real conception.

$DATA_{05}$ included 85,465 records (69% of the entire data). Here, all the 26 classes of parity*dim were represented, while only 28 of the 40 classes of year-season were enclosed, both the 2 classes of the status of the bull at breeding were reported. For random effect, 1,398 (vs1,400) herd levels, 83 (vs 86) technician levels, 450 (vs 513) sires of cow and 241 (vs 306) service sires were considered into analysis. Service sires averaged 355 records, the 50% of them had more than 160 observations.

Variance components and Heritability.

Tables 2 and 3 show variance components and heritabilities of every model for CR and NR respectively.

All variance components estimated were essentially low, in accordance with the difficult assessment of the factor affecting fertility from field data. Herd (σ^2_{he}) and technician (σ^2_{tc}) variances remained constant across traits and models, but herd variance was constantly higher that technician variance. Among the animal effects, in animal models direct genetic (σ^2_{dg}) was constantly the higher, followed by maternal genetic (σ^2_{mg}), while in sire models maternal environmental was the highest (σ^2_{me}). Direct environmental (σ^2_{de}) was low in sire models, as here the same effect of service sire was computed. The latter appeared to strongly decrease in models D actually. In animal models (with the embryo direct genetic effect), direct environmental accounted for higher variances, and direct genetic was less affected in models D. It should be noticed that direct-maternal covariance ($\sigma_{dg\text{-}mg}$) was essentially low for the most of the models.

Heritabilities for CR (from 0.011 to 0.119) were generally higher than those of NR (from 0.005 to 0.054). In CR, threshold models gave constantly higher heritabilities than linear models (from 0.018 to 0.119 *vs.* 0.011 to 0.081). The same happened for sire and animal models, were the latter gave higher h^2 (from 0.011 to 0.075 *vs.* 0.024 to 0.119) . The threshold animal model A gave the highest heritability (0.119). The biggest differences were anyway found among model specifications. In all the cases, models A gave the highest h^2, which decreased in models B when the environmental effect of the cow was included. In models C, the inclusion of maternal genetic effect and the estimation of direct-maternal covariance did not affect heritability significantly. In models D heritability strongly decreased, due to the addition of the service sire permanent environmental effect, which eroded direct genetic variance.

In NR heritability follows the same pattern among the models. Threshold models gave higher h^2 than linear models (from 0.010 to 0.054 *vs.* 0.005 to 0.041), as well as animal models resulted in higher values than sire models did (from 0.014 to 0.054 *vs.* 0.005 to 0.032). Again, the threshold animal model A gave the highest heritability (0.054). The biggest differences remained among model specifications. Models A gave the highest h^2, followed by models B. In models C were similar to models B, and in models D heritability significantly decreased.

Comparing the values found here with those reported in literature, Jansen (1986) found heritability ranging between 0.024 to 0.015 for CR and between 0.021 and 0.013 for NR with linear sire model estimating direct and maternal effects, while our values for the same model were 0.045 for CR and 0.020 for NR. For CR, both Kuhn and Hutchinson (2008) and Berry et al. (2010) found heritabilities below 0.01, so ours appears to be is the highest found with a comparable methodology, as only Nadarajah et al. (1988) found a 0.15 heritability via sire-son regression. For NR, Andersen-Ramberg et al., (2005) found values around 0.01 for direct heritability on heifers, while our comparable value was 0.02 .

For the comparison of linear and threshold models, our findings are in accordance to Weller and Ron (1992), Matos et al. (1997) and Weigel and Rekaya (2000), who found higher h^2 in threshold models for female fertility. About sire and animal models, Matos et al. (1997) working on Rambouillet and Finnsheep ovine breeds found heritabilities being higher in animal models than sire models, and in threshold models than linear models, similar to the pattern found here.

Goodness of fit and predictive ability

Goodness of fit - In tables 4 and 5 are reported values of MSE as indicator of goodness of fit for CR and NR, respectively. In every model values of MSE were smaller in NR, but it should considered the lower standard deviation of this trait (0.46 for NR, 0.50 for CR), so no differences are shown between the two traits. Among the models, although a well recognizable pattern is not evident and no particular difference is imputable to linear and threshold models, sire models gave significantly lower values of MSE. Among the model specification, models D+ fitted always better than the others, due to the sum of additive genetic and permanent environmental effects, and models D fitted worst than A, B, C, as these latter comprehended a part of permanent environmental variance into the additive genetic. Anyway, for both traits, linear sire model D+ gave the best possible fitting (0.179 for NR, 0.287 for CR), but, if we do not consider D+ models, linear sire model B was the best fitting model for both traits (0.201 for NR, 0.389 for CR).

Predictive ability - In tables 4 and 5 are reported the two values of χ^2 as indicator of predictive ability of the models in the 2 scenarios of prediction. In the first prediction (prediction of the unobserved), 65 service sires were estimated via relationship matrix with each model, they showed at least 100 observations in $DATA_{05}$ as all their records fell after year 2005. In the second prediction (prediction of proven), 38 were the service sires having at least 70 observations in $DATA_{05}$ and 30 observations in $DATA_{08}$.

In the first scenario, CR was much more predictable than NR, and this is in agreement with the heritability found. Although in NR the values of χ^2 were flat across the models, in CR animal models gave slightly better predictions than sire models, as expected. No differences were found between linear and threshold models, meaning that in this conditions violating assumption of linear model with binary observations does not affect significantly prediction via relationship matrix. No recognizable pattern is shown among the different model specifications, and it should be noticed that models D+ were not considered here as no prediction of the environmental effect of the service sire is available. Anyway, the best predictive model in this case was threshold animal model C for CR and threshold sire mode C for NR. To have an idea of the accuracy of prediction, as we did not use MSE in prediction (due to the binary variable), for the best predictive models we computed a number of wrong prediction on total predictions, as difference between expected and observed successful inseminations divided by total number of inseminations for that sire. Here, the mean value across the sires was 39% for threshold sire mode C applied on NR and 12% for threshold animal model C on CR.

In the second scenario, were the service sire outcome was predicted according to his observations previous to 2005, we see again that NR gives higher values of χ^2 than CR, but no differences can be underlined across the models within trait. Anyway, the best predictive models were linear sire model C for NR and linear animal model A for CR. Mean values for sires percentage of wrong predictions on total was 37% for NR and 13% for CR.

Unfortunately, there’s no comparable assessment of predictive ability for bull fertility conducted this way. Blaschek et al. (2011) found that accuracy of prediction was approximately 14.5% using high-density SNP genotypes, while Kuhn and Hutchinson (2008) found that correlation between predicted and observed bull fertility ranged between 38.1 and 28.3.

Conclusions

The aim of this study was to investigate the role of service sire in dairy cattle fertility, using the Brown Swiss populations reared in the province of Bolzano (North-Eastern alps of Italy). Variance components and predictive ability assessment of different models were carried out. Results showed that genetic variance for male fertility can be caught, with various models, but threshold models and animal models gave higher values of h^2. Other non-animal variance components showed to be of low significance in determining the outcome of the insemination, and herd effect explained more variance the technician effect. No particular evidence of different predictive ability arised between the models, suggesting that linear models can be reliable although violating assumptions, and sire models behave as good as animal models with the advantage of reducing computational time.

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Table 12: Descriptive statistics for whole dataset[1] ($DATA_{TOT}$) and calibration dataset[2] ($DATA_{05}$) used for obtaining service sires EBVs to be used in the cross-validation.

	$DATA_{TOT}$	$DATA_{05}$
Number of inseminations in dataset	124,206	85,465
Average conception rate (CR)	0.48	0.49
Average non-return at 56 days (NR)	0.70	0.70
% of discordant values	22	21
Number of service sires	306	241
Minimum number of ins. per service sire	100	1
Average number of ins. per service sire	406	355
Mean of average CR per service sire	0.455	0.463
Mean of average NR per service sire	0.692	0.690
Number of cows	28,873	23,912
Minimum number of ins. per cow	2	1
Number of sires of cow	514	450
Minimum number of ins. per sire of cow	20	1
Number of herds	1,400	1,398
Minimum number of ins. per herd	20	4
Number of technicians	86	83
Minimum number of ins. per technician	25	18

[1] Whole dataset refers to years 1999-2008.

[2] Calibration dataset referes to years 1999-2005. Minimun frequency for the random effects does not apply here.

Table 2: Estimates[1] of variance components and heritability for Conception Rate (CR) the different models[2] (in bold the higher h^2 value among the models).

	σ^2_{dg}	σ^2_{me}	σ^2_{mg}	$\sigma_{dg\text{-}mg}$	σ^2_{de}	σ^2_{he}	σ^2_{tc}	σ^2_{res}	h^2
Linear sire model									
A	0.0028					0.0035	0.0013	0.2410	0.045 (0.034 to 0.057)
B	0.0028	0.0098				0.0031	0.0014	0.2318	0.044 (0.033 to 0.057)
C	0.0028	0.0087	0.0015	-0.0004		0.0030	0.0014	0.2318	0.045 (0.034 to 0.058)
D	0.0007	0.0087	0.0015	-0.0004	0.0016	0.0030	0.0014	0.2318	0.011 (0.002 to 0.025)
Linear animal model									
A	0.0204					0.0031	0.0014	0.2269	0.081 (0.068 to 0.094)
B	0.0118	0.0068				0.0030	0.0014	0.2266	0.047 (0.038 to 0.058)
C	0.0110	0.0039	0.0101	-0.0063		0.0028	0.0014	0.2267	0.042 (0.034 to 0.051)
D	0.0061	0.0042	0.0083	-0.0034	0.0011	0.0028	0.0014	0.2288	0.024 (0.014 to 0.037)
Threshold sire model									
A	0.0196					0.0229	0.0090	1	0.075 (0.057 to 0.095)
B	0.0205	0.0668				0.0218	0.0096	1	0.073 (0.055 to 0.095)
C	0.0210	0.0587	0.0107	-0.0032		0.0212	0.0097	1	0.075 (0.057 to 0.095)
D	0.0052	0.0588	0.0106	-0.0026	0.0119	0.0213	0.0097	1	0.018 (0.004 to 0.043)
Threshold animal model									
A	0.1392					0.0222	0.0100	1	**0.119 (0.102 to 0.137)**
B	0.0837	0.0472				0.0215	0.0100	1	0.072 (0.058 to 0.087)
C	0.0775	0.0278	0.0676	-0.0420		0.0203	0.0101	1	0.062 (0.050 to 0.074)
D	0.0401	0.0280	0.0600	-0.0245	0.0093	0.0200	0.0099	1	0.034 (0.018 to 0.049)

[1] Estimates ar the means of the marginal posterior densities for variance components and the mean (with 95% Highest Probability Density Intervals) for the heritability.

[2] Models A, B, C, and D differ in specifications. All the account for the fixed effects of parity-dim at insemination, year-season of insemination, status of the service sire at insemination; and the random effects of herd and technician. Model A includes the direct additive genetic effect, in model B the maternal environmental effect is added, in model C the direct maternal effect in included, and in model C the direct environmental effect of the service sire is added.

Table 3: Estimates[1] of variance components and heritability for Conception Rate (NR) the different models[2] (in bold the higher h^2 value among the models).

NR	σ^2_{dg}	σ^2_{me}	σ^2_{mg}	$\sigma_{dg\text{-}mg}$	σ^2_{de}	σ^2_{he}	σ^2_{tc}	σ^2_{res}	h^2
Linear sire model									
A	0.0011					0.0041	0.0008	0.2045	$0.020^{(0.013 \text{ to } 0.028)}$
B	0.0010	0.0054				0.0036	0.0008	0.1994	$0.020^{(0.013 \text{ to } 0.028)}$
C	0.0010	0.0050	0.0005	0.0000		0.0036	0.0008	0.1994	$0.020^{(0.013 \text{ to } 0.028)}$
D	0.0003	0.0050	0.0005	0.0000	0.0006	0.0036	0.0008	0.1994	$0.005^{(0.001 \text{ to } 0.013)}$
Linear animal model									
A	0.0086					0.0038	0.0008	0.1984	$0.041^{(0.031 \text{ to } 0.050)}$
B	0.0043	0.0042				0.0036	0.0008	0.1976	$0.021^{(0.015 \text{ to } 0.027)}$
C	0.0046	0.0030	0.0036	-0.0023		0.0035	0.0008	0.1973	$0.022^{(0.015 \text{ to } 0.028)}$
D	0.0030	0.0032	0.0029	-0.0012	0.0004	0.0035	0.0008	0.1980	$0.014^{(0.008 \text{ to } 0.022)}$
Threshold sire model									
A	0.0085					0.0361	0.0066	1	$0.032^{(0.021 \text{ to } 0.045)}$
B	0.0085	0.0438				0.0335	0.0068	1	$0.031^{(0.020 \text{ to } 0.044)}$
C	0.0086	0.0402	0.0045	-0.0003		0.0333	0.0068	1	$0.032^{(0.021 \text{ to } 0.044)}$
D	0.0026	0.0401	0.0044	-0.0001	0.0052	0.0332	0.0068	1	$0.010^{(0.002 \text{ to } 0.024)}$
Threshold animal model									
A	0.0595					0.0349	0.0070	1	$\mathbf{0.054^{(0.043 \text{ to } 0.066)}}$
B	0.0325	0.0349				0.0332	0.0070	1	$0.029^{(0.022 \text{ to } 0.038)}$
C	0.0327	0.0249	0.0273	-0.0147		0.0325	0.0069	1	$0.029^{(0.021 \text{ to } 0.037)}$
D	0.0198	0.0248	0.0258	-0.0094	0.0039	0.0325	0.069	1	$0.018^{(0.001 \text{ to } 0.026)}$

[1] Estimates ar the means of the marginal posterior densities for variance components and the mean (with 95% Highest Probability
Density Intervals) for the heritability.

[2] Models A, B, C, and D differ in specifications. All the account for the fixed effects of parity-dim at insemination, year-season of insemination, status of the service sire at insemination; and the random effects of herd and technician. Model A includes the direct additive genetic effect, in model B the maternal environmental effect is added, in model C the direct maternal effect in included, and in model C the direct environmental effect of the service sire is added.

Table 4: Summary of statistics for the future-year cross-valiadation applied to Conception Rate (CR). Values referring to the respective best model[1] in boldface.

[1]If D+ model(s) shows best values, best model escluding D+ is highlighted as well.

Model[2]	Goodness of fit[3]	Prediction[4] of young bulls[5]	Prediction[4] of proven bulls[6]
Linear sire model			
A	0.396	227,051	1,406,781
B	**0.389**	179,540	1,248,159
C	0.398	208,807	1,585,148
D	0.658	148,563	1,298,954
D+	**0.287**	.	**1,385,480**
Linear animal model			
A	0.438	145,484	**1,209,678**
B	0.530	148,712	1,309,535
C	0.617	149,113	1,320,009
D	0.811	150,805	1,252,698
D+	0.405[1]	.	1,285,938
Threshold sire model			
A	0.394	175,237	1,280,834
B	0.428	265,622	1,601,905
C	0.417	225,442	1,371,812
D	0.634	150,835	1,489,104
D+	0.335	.	1,343,881
Threshold animal model			
A	0.458	151,851	1,380,386
B	0.483	148,286	1,303,528
C	0.624	**142,084**	1,339,386
D	0.931	147,400	1,360,875
D+	0.468	.	1,568,211

[2]Models A, B, C, and D differ in specifications. All the account for the fixed effects of parity-dim at insemination, year-season of insemination, status of the service sire at insemination; and the random effects of herd and technician. Model A includes the direct additive genetic effect, in model B the maternal environmental effect is added, in model C the direct maternal effect in included, and in model C the direct environmental effect of the service sire is added.

[3]Mean square error estimated via non-parametric local weighted regression of raw CR on estimated breeding values (EBV) of the sire for each model.

[4] Sum of $\chi2$ statistics across service sires, based on the comparison between the predicted and observed outcome of the insemination for each service sire.

[5] Based on service sires estimated via relationship matrix in calibration dataset and validated accordingly to their inseminations in validation dataset (*n*=65).

[6] Based on service sires estimated on a minimum of 70 inseminations in calibration dataset and 30 inseminations in validation dataset (*n*=38).

Table 5: Summary of statistics for the future-year cross-valiadation applied to Non-Return at 56 days (NR). Values referring to the respective best model[1] in boldface.

[1] If D+ model(s) shows best values, best model escluding D+ is highlighted as well.

Model[2]	Goodness of fit[3]	Prediction[4] of young bulls[5]	Prediction[4] of proven bulls[6]
Linear sire model			
A	0.209	1,897,738	1,296,5985
B	**0.201**	1,897,873	1,335,0601
C	0.205	1,978,113	**1,263,7074**
D	0.351	1,911,911	1,335,4068
D+	**0.179**	.	1,307,1610
Linear animal model			
A	0.302	1,935,870	1,337,5111
B	0.480	1,897,015	1,315,8727
C	0.486	1,893,596	1,323,3559
D	0.516	1,888,147	1,327,0477
D+	0.337	.	1,326,9724
Threshold sire model			
A	0.214	1,897,515	1,317,6413
B	0.222	1,904,985	1,235,7952
C	0.245	**1,886,448**	1,315,4711
D	0.372	1,893,592	1,302,4912
D+	0.184	.	1,314,8013
Threshold animal model			
A	0.370	1,899,008	1,321,7331
B	0.468	1,898,438	1,324,7295
C	0.468	1,899,847	1,300,1240
D	0.597	1,896,690	1,283,7951
D+	0.359	.	1,265,6554

[2] Models A, B, C, and D differ in specifications. All the account for the fixed effects of parity-dim at insemination, year-season of insemination, status of the service sire at insemination; and the random effects of herd and technician. Model A includes the direct additive genetic effect, in model B the maternal environmental effect is added, in model C the direct maternal effect in included, and in model C the direct environmental effect of the service sire is added.

[3] Mean square error estimated via non-parametric local weighted regression of raw CR on estimated breeding values (EBV) of the sire for each model.

[4] Sum of $\chi 2$ statistics across service sires, based on the comparison between the predicted and observed outcome of the insemination for each service sire.

[5] Based on service sires estimated via relationship matrix in calibration dataset and validated accordingly to their inseminations in validation dataset (*n*=65).

[6] Based on service sires estimated on a minimum of 70 inseminations in calibration dataset and 30 inseminations in validation dataset (*n*=38).

Chapter three

Genetic analysis of fertility in the Italian Brown Swiss population using different models and trait definitions

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Abstract

The aim of this study was to estimate genetic parameters for fertility and production traits in the Brown Swiss population reared in the Alps (Bolzano-Bozen province, Italy). Fertility indicators were: interval from parturition to first service, interval from first service to conception, and interval from parturition to conception either expressed as days (iPF, iFC, and iPC, respectively) and as number of potential 21-d estrus cycles (cPF, cFC, and cPC, respectively); number of inseminations to conception (INS); conception rate at first service (CFS); and non-return rate at 56 d post-first service (NR56). Production traits were: peak milk yield (pMY), lactation milk yield (lMY), lactation length (LL), average lactation protein percentage (PP), and average lactation fat percentage (FP). Data included 71,556 lactations (parities 1 to 9) from 29,582 cows reared in 1,835 herds. Animals calved from 1999 to 2007 and were progeny of 491 AI bulls. Gibbs sampling and Metropolis algorithms were implemented to obtain (co)variance components using both univariate and bivariate censored threshold and linear sire models. All the analyses accounted for parity and year-month of calving as fixed effects, and herd, permanent environmental cow, additive genetic sire, and residual as random effects. Heritability estimates for fertility traits ranged from 0.030 (iFC) to 0.071 (cPC). Strong genetic correlations were estimated between iPF and cPF (0.97), and iPC and cPC (0.96). Estimate of heritability for cFC (0.055) was approximately double compared with iFC (0.030), suggesting that measuring the elapsed time between first service and conception in days or potential cycles is not equivalent; this was also confirmed by the genetic correlation between iFC and cFC, which was strong (0.85), but more distant from unity than the other two pairs of fertility traits. Genetic correlations between INS, CFS, NR56, cPF, cFC, and cPC ranged from 0.07 to 0.82 as absolute value. Fertility was unfavorably correlated with production; estimates ranged from -0.26 (cPC with PP) to 0.76 (cPC with LL), confirming the genetic antagonism between reproductive efficiency and milk production. Although heritability for fertility is low, the contemporary inclusion of several reproductive traits in a merit index would help to improve performance of dairy cows.

Key words: censored, dairy cow, fertility, genetic parameter.

Introduction

Female fertility is a complex trait and comprises the ability of the cow to return in heat within an acceptable period after calving, to show heat in a proper manner, and to become pregnant with a limited number of inseminations (Groen et al., 1997). A relevant body of literature links selection for milk yield traits to a general loss of reproductive fitness, health and longevity (Dematawewa and Berger, 1998; Lucy, 2001; Wall et al., 2003), and the genetic antagonism between yield and fertility has often been indicated as the major factor leading to hampered reproductive performance (Hansen et al., 1983; Oltenacu et al., 1991).

The decline in fertility has supposedly come from an increase of energy utilization from the mammary gland and a subsequent amended hormonal and metabolic profile. This might have an influence on the reproductive organs, leading to low ovulation rates, weak estrus and decreased success in embryo establishment (Veerkamp et al., 2003). Although losses of reproductive efficiency have been relevant in the major dairy populations (Hare et al., 2006), several authors reported that the genetic improvement of fertility is viable (Andersen-Ranberg et al., 2005; Holtsmark et al., 2008; Heringstad and Larsgard, 2010). Fertility traits are usually characterized by low heritability and they are often more influenced by non-additive than additive genetic effects (Fuerst and Sölkner, 1994).

Predicted breeding values for reproductive performance often rely on calving interval, i.e., the time between two subsequent calvings. This trait is easier to record and is much less affected by data quality than other measures of fertility such as number of inseminations to conception (**INS**) and conception rate at first service (**CFS**). However, it is not available for cows culled before subsequent calving, leading to overestimation of reproductive efficiency. Also, calving interval is a late measure of fertility as it is available approximately one year after the beginning of estrus activity with a delayed publication of breeding values for progeny tested bulls. Because of these limitations, efforts are needed to look for related traits which could be useful as early indicators of reproductive efficiency (Berry et al., 2003; Dal Zotto et al., 2007; König et al., 2008).

The use of direct measures of fertility other than calving interval could lead to more timely results in breeding programs, provided that phenotypic data are reliable and that they are modeled correctly. Non-return rate at 56 d post-first service (**NR56**) is one of the most used traits as it allows for a fast evaluation of reproduction performance, without the need of waiting for the subsequent calving; it is commonly taken into account both to infer genetic parameters for fertility in dairy cows (Jamrozik et al., 2005; König et al., 2008) and to routinely evaluate bulls on a national (Andersen-Ranberg et al., 2005; Gredler et al., 2007; Miglior, 2007) and an international basis

(Biffani and Canavesi, 2007). An important drawback of NR56 is that it considers successful those inseminations which are not followed by a subsequent breeding within 56 d, without validation through subsequent calving.

One of the major limitations with fertility is that it cannot be fully represented by a single measure, but rather by a complex of measures, including non-normal and categorical traits. Conception rate at first service and NR56 are dichotomous variables, and INS is a count and highly skewed trait. The intervals between parturition to first service (**iPF**), first service to conception (**iFC**), and parturition to conception (**iPC**) are conceptually based on a categorical number of estrus cycles and are again characterized by highly skewed distribution. Furthermore, not all estrus cycles lead to an insemination because of voluntary waiting period, non observed heat, and health disorders; not all inseminations result in a conception because of infertility issues; and not all conceptions lead to a subsequent calving because of abortions, death of the cow or, simply, lack of information. All these aspects reinforce the complexity of defining reproduction efficiency. Finally, the beginning and end of each estrus cycle are not regularly recorded at the population level and insemination and parturition information is sometimes lacking as well (censored data). Modeling the intervals in terms of number of potential 21-d cycles and use of censored threshold models has been recently proposed to overcome some of these limitations (Chang et al., 2007).

In Bolzano-Bozen province (north-eastern Italian Alps), an efficient AI recording scheme is currently running and the majority of inseminations are carried out by veterinarians. The Brown Swiss is the most important breed of this province and accounts for approximately 41% of cows involved in monthly test-day milk recording. On a national basis, the province represents about 25% of the whole Brown Swiss population enrolled in the milk recording scheme. Italian Brown Swiss has been characterized for several important production aspects such as milk coagulation properties (De Marchi et al., 2007) and yield and quality of cheese (De Marchi et al., 2008). However, information on genetic aspects of female fertility within the population is scarce and limited to calving interval (Dal Zotto et al., 2007) or to success rate (Rizzi et al., 2009). Outside Italy, Brown Swiss breed has been studied for fertility in Germany (Distl, 1991), Austria (Fuerst and Sölkner, 1994), and Mexico (Estrada-León et al., 2008).

The aim of this study was to infer (co)variance components and related parameters for several fertility traits using censored linear and threshold models, and to estimate genetic correlations between fertility and production in the Italian Brown Swiss population.

Materials and Methods

Data Collection and Editing Procedure

Insemination and production records on Brown Swiss cows were obtained from the Breeders Association of Bolzano-Bozen province (Italy). Data included 71,556 lactations from 29,582 cows (parities 1 to 9) reared in 1,835 herds; animals calved from 1999 to 2007 and were progeny of 491 AI bulls. In order to limit the potential effect of selection bias due to culling for both production and fertility issues, sequential edits was applied and second and later lactations were only retained if a first-lactation record was available. Following this approach, distribution of data across parities was as follows: 29,582 records on first lactation, 19,140 on second lactation, 11,360 on third lactation, and 11,474 on fourth and later lactations. Production traits considered were peak milk yield (**pMY**, kg), lactation milk yield (**lMY**, kg), lactation length (**LL**, d), average lactation protein percentage (**PP**, %), and average lactation fat percentage (**FP**, %). Fertility traits included both success and interval indicators. Success traits were INS, CFS and NR56. The first one was coded as an ordinal categorical variable according to the number of services needed to achieve pregnancy, and inseminations occurring within 6 d were considered as a single service. The variable consisted of five classes, the last being an open class including lactations with more than 4 services. Conception rate at first service and NR56 were coded as dichotomous variables according to the achievement of pregnancy at first service for CFS, or the occurrence of a second breeding within 56 d after first service (0) or not (1) for NR56. Records for INS were considered censored if subsequent calving was not recorded or more than 4 services occurred. Traits iPF, iFC, and iPC were edited as follows: between 21 and 252 d for iPF (i.e., 12 twenty-one-day cycles), between 0 and 336 d for iFC (i.e., 16 twenty-one-day cycles), and between 21 and 336 d for iPC (i.e., 16 twenty-one-day cycles); iFC and iPC were considered censored if a subsequent calving was not recorded. In addition, number of potential cycles from parturition to first service (**cPF**), from first service to conception (**cFC**), and from parturition to conception (**cPC**) were calculated from iPF, iFC, and iPC, respectively. The 3 categorical variables were represented by 8 longitudinal 21-d classes. For cPF and cPC, the 21-d intervals started from the edited minimum of 21 d after calving, so that the first class grouped records between 21 and 42 d, the second between 43 and 64 d, and so on up to the 8th class. For cFC all records for iFC = 0 (cows pregnant at first service) were grouped in the first class, the second class grouped records for iFC between 7 and 33 d, and the third and subsequent classes grouped records in 21-d classes starting from iPF = 33 d. Records exceeding 8 cycles were clustered into the 8th class and treated as censored, besides the censoring criterion for the respective days-measured trait (missing subsequent calving for iFC and iPC). Figures 1, 2, and 3 depict the distributions and 21-d clustering of iPF and cPF, iFC and cFC, and iPC and cPC, respectively.

Herds with less than 5 observations were discarded as well as cows that moved to a different herd during the breeding period within a given lactation. Sires were required to have a minimum of 10 observations distributed across at least 3 herds and 3 daughters.

Statistical analysis

Univariate Censored Linear Model. A mixed censored linear model (Carriquiry et al., 1987; Sorensen et al., 1998; Guo et al., 2001) was used for the analysis of production and days-measured interval traits (i.e., iPF, iFC, and iPC). The model may be written as:

$$y_i = x_i'\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s} + e_i,$$

where y_i is the observed (noncensored record) of cow i; $x_i', z_{h,i}', z_{p,i}'$, and $z_{s,i}'$ are incidence vectors related to location vector β(parity effect: 4 classes with the last class including parities 4 to 9; year-month of calving effect: 108 classes), **h** (herd effect), **p** (permanent environmental effect of the cow), and **s** (sire transmitting abilities), respectively; and e_i is the residual. Unobserved responses for censored records can be augmented using a truncated normal process as:

$$\tilde{y}_c \sim N\left(x_c'\beta + z_{h,c}'\mathbf{h} + z_{p,c}'\mathbf{p} + z_{s,c}'\mathbf{s}, \sigma_c^2\right) I(y_c, \infty),$$

where y_c is the observed censoring time, such that the augmented values are larger than the censoring point.

Univariate Censored Threshold Model. The threshold model was used for the analysis of cycles-measured traits (i.e., cPF, cFC, and cPC) which were treated as ordinal categorical variables with 8 classes and 7 thresholds, and INS, CFS and NR56 which were ordinal categorical and binary (0/1) variables as previously described. The threshold model postulates a mixed effect model in the scale of a latent variable, liability (λ), for each observation (Gianola, 1982; Gianola and Foulley, 1983). The observation takes the value j only if λ is greater than or equal to T_{j-1} and smaller than T_j, where T_{j-1} and T_j are unknown thresholds. The probability model can be written as:

$$\text{Prob}(y_i = j|\beta, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}) = \Phi\left[T_j - \left(x_i\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right]$$
$$-\Phi\left[T_{j-1} - \left(x_i\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right],$$

where j = 1, 2,…, j indexing the category in which the observation belongs; $\Phi(\cdot)$ is the standard cumulative normal distribution function, and $\mathbf{T} = \left[\mathrm{T_0}, \mathrm{T_1}, \mathrm{T_2}, \dots, \mathrm{T_j}\right]'$ is the vector of unknown thresholds. The thresholds must satisfy $-\infty = \mathrm{T_0} \leq \mathrm{T_1} \leq \mathrm{T_2} \leq \dots, \leq \mathrm{T_j} = \infty$. The first threshold $\mathrm{T_1}$ is set to zero, because the parameter cannot be identified in a probit analysis. This concept, as previously reported by Chang et al. (2006), accommodates situations in which records are censored at the last observed point. If an observation is censored at the *j*th insemination, and its status is not pregnant, then its corresponding liability must be larger than T_j. The probability that the observation is censored at the *j*th category is:

$$\mathrm{Prob}(y_i = j, \text{censored} \mid \beta, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}) = 1 - \Phi\left[T_j - \left(x_i'\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right].$$

The joint probability of N noncensored and censored data, given the location effects and the thresholds, is:

$$\begin{aligned}&\mathrm{Prob}(\mathbf{y} \mid \beta, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}, \boldsymbol{\delta}) \\ &= \prod_{i=1}^{N} \left\{\Phi\left[\mathrm{T}_{y_i} - \left(x_i'\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right]\right. \\ &\left. - \Phi\left[\mathrm{T}_{y_i-1} - \left(x_i'\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right]\right\}^{1-\delta_i} \left\{1\right. \\ &\left. - \Phi\left[\mathrm{T}_{y_i-1} - \left(x_i'\beta + z_{h,i}'\mathbf{h} + z_{p,i}'\mathbf{p} + z_{s,i}'\mathbf{s}\right)\right]\right\}^{\delta_i}\end{aligned}$$

where δ is the vector of censoring indicators; $\delta_i = 0$ if a record is not censored and 1 otherwise.

Bivariate Censored Threshold-Linear and Threshold-Threshold Model. A Bayesian bivariate model was used to infer genetic relationship between fertility traits and between fertility and productions traits. (Co)variance components were obtained fitting threshold-linear (Foulley et al., 1983), and threshold-threshold models (König et al., 2008). Criteria for censoring were the same as in the univariate approach. Right-censored records were included as unknown parameters in the model, using the methodology described by Guo et al. (2001) which is based on a data augmentation procedure (Tanner and Wong, 1987). Systematic effects were the same as for univariate analyses. Flat priors were used for systematic effects and dispersion parameters. Prior distributions for the additive genetic, permanent environmental cow and herd effects were normal densities. In a Bayesian setting, we assumed:

$$\begin{bmatrix}\mathbf{s}_1 \\ \mathbf{s}_2\end{bmatrix} \sim N(\mathbf{0}, \mathbf{G} \otimes \mathbf{A}) \text{ ,}$$

where $\mathbf{G}\begin{bmatrix}\sigma_{s1}^2 & \sigma_{s12} \\ \sigma_{s12} & \sigma_{s2}^2\end{bmatrix}$ is a 2 x 2 sire transmitting abilities (co)variance matrix, and A is the numerator relationship matrix between sires. Likewise, permanent environmental cow and herd effects were assumed to follow a multivariate normal distribution:

$$\begin{bmatrix}\mathbf{p}_1 \\ \mathbf{p}_2\end{bmatrix} \sim N(\mathbf{0}, \mathbf{P} \otimes \mathbf{I})$$

$$\begin{bmatrix}\mathbf{h}_1 \\ \mathbf{h}_2\end{bmatrix} \sim N(\mathbf{0}, \mathbf{H} \otimes \mathbf{I})$$

where $\mathbf{P}\begin{bmatrix}\sigma_{p1}^2 & \sigma_{p12} \\ \sigma_{p12} & \sigma_{p2}^2\end{bmatrix}$ was a 2 x 2 permanent environmental (co)variance matrix and $\mathbf{H}\begin{bmatrix}\sigma_{h1}^2 & \sigma_{h12} \\ \sigma_{h12} & \sigma_{h2}^2\end{bmatrix}$ was a 2 x 2 (co)variance matrix between herd effects for the 2 traits.

Residuals for linear traits were assumed correlated and normally distributed, $\boldsymbol{e} \sim N(0, \mathbf{R_0} \otimes \mathbf{I})$, R_0 being the residual (co)variance matrix:

$$\mathbf{R}_0 = \begin{bmatrix}\sigma_{e1}^2 & \sigma_{e12} \\ \sigma_{e21} & \sigma_{e2}^2\end{bmatrix},$$

where σ_{e1}^2 and σ_{e2}^2 are the variances of trait 1 and 2, respectively, and σ_{e12} (or σ_{e21}) is the covariance between the traits. Residual variances were forced to 1 in case of threshold analysis, so that for threshold-linear models the matrix was:

$$\mathbf{R}_0 = \begin{bmatrix}1 & \sigma_{e12} \\ \sigma_{e21} & \sigma_{e2}^2\end{bmatrix}$$

Finally, for threshold-threshold analysis the residual matrix was:

$$\mathbf{R}_0 = \begin{bmatrix}1 & \sigma_{e12} \\ \sigma_{e21} & 1\end{bmatrix}$$

Gibbs sampler. Gibbs sampling and Metropolis algorithm were implemented for Gaussian and categorical variables, respectively. Such algorithms were extensively detailed in Chang et al. (2006) for censored linear, censored threshold and bivariate censored threshold-linear model, and in König et al. (2008) for threshold-threshold model. All analyses were performed using software previously developed by Y. M. Chang for similar analyses (Chang et al., 2006). A single Gibbs chain of 250,000 samples was obtained for univariate models while for bivariate models 550,000 iterations were run, discarding the first 50,000 samples as burn-in. The effective length of the burn-in and the chain size were chosen on the basis of the methods of Raftery and Lewis (1992) and Geyer (1992), respectively. Sample values were saved every 20 iterations for univariate model and 50 iterations for bivariate models. The posterior mean was used as a point estimate of (co)variance components and related parameters. Lower and upper bounds of the 95% highest posterior probability density regions for heritabilities and additive genetic correlations were estimated from the Gibbs samples.

Heritability was computed as:

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_p^2 + \sigma_h^2 + \sigma_e^2}$$

Intra-herd heritability was calculated as:

$$h^2_{IH} = \frac{4\sigma^2_s}{\sigma^2_s + \sigma^2_p + \sigma^2_e}$$

Herd effect was defined as:

$$h^2_{he} = \frac{\sigma^2_h}{\sigma^2_s + \sigma^2_p + \sigma^2_h + \sigma^2_e}$$

Permanent environmental cow effect was computed as:

$$h^2_{pe} = \frac{\sigma^2_p}{\sigma^2_s + \sigma^2_p + \sigma^2_h + \sigma^2_e}$$

and genetic correlations were calculated as:

$$\rho_g = \frac{\mathrm{cov}_s(x,y)}{\sigma_{s,x}\sigma_{s,y}}$$

Results and Discussion

Fertility Traits

Means for fertility traits of Brown Swiss cows (Table 1) were more favorable than values previously reported for Holstein Friesians (Dematawewa and Berger, 1998; Berry et al., 2003; Wall et al., 2003), but similar to those reported for other breeds (Andersen-Ranberg et al., 2005; Gredler et al., 2007; Holtsmark et al., 2008). Phenotypic means for fertility in Brown Swiss cows from the present study were different from those reported by Estrada-León et al. (2008) on the same breed in the tropics of Mexico; in particular, the interval between parturition to conception in Estrada-León et al. (2008) was much more unfavorable (172.8 d) compared with our study (124.0 d; Table 1), and showed approximately twice SD than our findings (117.2 vs. 63.9 d). These results suggest that the environment plays an important role on fertility and that the difference between genotype by environment interaction may exist when comparing data from different rearing conditions.

Estimates of (co)variance components and related parameters are shown in Tables 2 and 3, respectively. Fertility traits can be split into three groups: the first includes information on the interval from parturition to first service (iPF and cPF); the second includes information on insemination events (iFC, cFC, INS, CFS, and NR56); and the third includes information on the interval from parturition to conception (iPC and cPC). Results will be discussed according to this grouping.

First Group: Parturition to First Service. The interval from parturition to first service averaged 88.2 d with SD of 37.3 d (Table 1), and the corresponding values of cPF were 3.64 and 1.67. Heritability and intra-herd heritability estimates for iPF and cPF were similar (0.049 and 0.058, and 0.058 and 0.068, respectively; Table 3). These traits showed quite large herd and permanent environmental cow effects (12.1 to 15.0% of the phenotypic variance), probably because of important differences in voluntary waiting period among different farms (Gallo et al., 2008) and among cows within farms. The genetic (phenotypic) correlations of 0.97 (0.99) between iPF and cPF (Table 4) were close to unity, suggesting that these two variables are essentially the same indicator of fertility. The distribution of records across days from parturition to first service is continuous and cyclic patterns are not evident (Figure 1); this is because the interval is the result of a certain number of estrus cycles, dependant from the voluntary waiting period and the estrus detection rate, but also from the post-parturition anestrous period. Estimates of heritability for iPF are higher than those reported by González-Recio et al. (2006) on Spanish Holsteins and by Estrada-León et al. (2008) on Mexican Brown Swiss cows, but lower than values obtained by Gredler et al. (2007) in dual purpose Austrian Simmental, and by König et al. (2008) on German Holstein cows. No estimates of heritability for cPF are currently available that the authors are aware of.

Second Group: Insemination Events. Non-return rate at 56 d post-first service averaged 0.71 (Table 1) and exhibited the lowest heritability (approximately 0.04; Table 3) among categorical traits, and often the weakest correlations with other measures of fertility (Table 4). Nevertheless, estimates of heritability for NR56 are higher than those reported by Gredler et al. (2007), who calculated a value of 0.011 with linear models, and König et al. (2008), who reported a value of 0.029 from binary threshold models. Mean value for CFS, validated by subsequent calving, was much lower than NR56 (0.45 and 0.71, respectively; Table 1), confirming that the latter trait largely overestimates fertility. Also, heritability and intra-herd heritability for CFS were higher than NR56 (0.055 and 0.058 vs. 0.037 and 0.039, respectively). These two traits are calculated through different procedures (the occurrence of a second insemination within 56 d for NR56, and the subsequent calving for CFS), and results from this study let us to infer that they can not be considered as indicators of the same fertility trait. Number of inseminations to conception averaged 1.74 (Table 1), but it should be noted the high incidence of censored records (23.4%) for this trait. Heritability estimate was 0.058 (Table 3), and phenotypic and genetic correlations with other fertility traits were moderate to strong, with few exceptions (Table 4). In general, NR56, CFS, and INS showed moderate to low and unfavorable genetic correlations with cPF (Table 4). Genetic and phenotypic correlations between INS and CFS were -0.78 and -0.73, respectively; the strong relationship between these traits was expected as CFS is a clustering of INS (CFS = 1 for INS = 1, CFS = 0 for INS > 1). Several studies on Holstein Friesian and Norwegian Red breeds reported values of heritability for INS comprised between 0.01 and 0.04 when estimated using linear models (Dematawewa and Berger, 1998; Wall et al., 2003; Sun et al., 2010), and around 0.04 when estimated through a threshold model (Chang et al., 2006; González-Recio et al., 2006).

The iFC averaged 36.0 d, with very large variability, and the corresponding cFC was 2.56 (Table 1). Heritability estimates for cFC (0.055; HPD95% = 0.041 to 0.072) were notably higher than iFC (0.030; HPD95% = 0.020 to 0.043). As expected, genetic and phenotypic correlations between the two variables were high (0.85 and 0.87, respectively), but significantly lower than between iPF and cPF (Table 4). Thus, iFC and cFC can not be considered as the same indicator of fertility. Differences might perhaps be due to data modeling, exacerbated by the skewed distribution of iFC. The pattern for iFC is peculiar: the interval between first insemination and conception for about half of the cows is zero (cows pregnant at first insemination) and for remaining cows is clearly cyclic (Figure 2).

Third Group: Parturition to Conception. The iPC is the sum of previously described interval traits, namely iPF and iFC (Figure 3), and averaged 124.0 d with SD of 63.9 d (Table 1). Heritability for iPC (0.060) and cPC (0.071) were similar (Table 3), and genetic (0.96) and phenotypic (0.95) correlations were close to unity (Table 4). Furthermore, management practices seem to have moderate influence on the traits as outlined by the herd effect, whereas permanent environmental cow was quite relevant (Table 3). Both iPC and cPC showed high relationships with other fertility traits but NR56, with the absolute value of the estimates comprised between 0.48 to 0.79 for phenotypic, and between 0.64 and 0.83 for genetic correlations (Table 4). Again, this is not surprising as iPC and cPC are the result of all other fertility measures. Heritability estimate for iPC is higher than that reported by González-Recio et al. (2006) on Spanish Holsteins and by Estrada-León et al. (2008) on Brown Swiss in the tropics. Regarding cycle-measured variables, Chang et al. (2007) reported heritability of 0.053 for the number of periods needed to achieve pregnancy in Norwegian Reds, slightly lower than our estimate.

Relationship With Production Traits

Means for production traits of Brown Swiss cows (Table 1) resembled those previously reported by Dal Zotto et al. (2007) and Cecchinato et al. (2009) on the same breed, whereas milk yield was lower and milk contents higher than values from Holstein Friesians (González-Recio et al., 2006; Cassandro et al., 2008).

Heritability for lMY (0.095) was lower than estimates from other studies on the same breed, whereas estimates for FP (0.284) and PP (0.318) were comparable to previous researches (Santus et al., 1993; Samoré et al., 2010). Management practices have higher influence on production than fertility traits as shown by herd effect (Table 3), leading to larger differences between heritability and intra-herd heritability. Our results are in agreement with findings from González-Recio et al. (2006) who assessed a value of 0.20 for herd effect on lMY, very similar to our estimate (0.264). Genetic relationships between fertility and production are reported in Table 5; cPF, cFC, cFP, and INS were positively related to pMY, lMY, and LL with estimates comprised between 0.24 and 0.76, confirming the genetic antagonism between fertility and production. Phenotypic correlations were similarly unfavorable, except for the estimate between cPF and pMY. Finally, phenotypic and genetic correlations between milk quality traits and fertility were low (-0.26 to 0.13; Table 5). Peak milk yield reflects the production potential of the cow at the usual time of insemination, whereas lMY measures the amount of milk produced by the animal during the entire lactation, and it is affected by the competition of the pregnancy eventually established or by the possible lactation elongation resulting from low fertility of the cow. Thus, pMY mainly describes the negative effect of production on fertility caused by the shrinkage of metabolites to the mammary gland at the expenses of the reproductive organs (Veerkamp et al., 2003), whereas lMY outlines the effect of fertility on production. González-Recio et al. (2006) reported genetic correlation of 0.16 between INS and lMY, lower than the value from our study, and König et al. (2008) estimated a genetic correlation of 0.14 between days to first service and lMY, much lower than the value between cPF and lMY form our work.

Conclusions

Despite low, results showed that exploitable genetic variation for fertility in the Italian Brown Swiss population exists. Heritability estimates were higher for cycles- than days-measured traits, probably due to the different methods used to assess dispersion parameters; in fact, linear models were applied to continuous variables, whereas threshold models were adopted to analyze cycles-traits. In the case of the interval between first service and conception, the use of potential cycles to express the trait was more appropriate than the use of continuous information; in fact, this interval showed a peculiar skewed distribution which made it more suitable to be analyzed as cycle-trait through threshold than linear models. An unfavorable relationship between fertility and production has been found; this explains the loss of fertility occurring in dairy cattle populations undergoing selection for production traits, even if reared in less intensive farming conditions such as the Bolzano-Bozen province. (Co)variance components obtained in the present study can be used to predict the genetic merit of sires for several direct measures of fertility and to improve reproductive efficiency of the population via selection. Further research is needed to investigate how fertility traits can be included in a merit index aiming at reversing the deterioration of reproduction efficiency in Brown Swiss breed. The use of genomic information could be also considered in addition to phenotypic data thus facilitating the dissection of this complex trait and its genetic improvement.

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Table 1. Descriptive statistics of fertility and production traits, and percentage of censored records

Trait[1]	Mean	SD	Minimum	Maximum	Censored records (%)
Fertility traits					
iPF, d	88.2	37.3	21	252	0
cPF, n	3.64	1.67	1	8	2.39
NR56	0.71	0.46	0	1	0
CFS	0.45	0.50	0	1	0
INS, n	1.74	1.02	1	5	23.4
iFC, d	36.0	55.4	0	314	16.9
cFC[2], n	2.56	2.25	1	8	20.2
iPC, d	124.0	63.9	21	336	16.9
cPC, n	4.91	2.16	1	8	28.5
Production traits					
pMY, kg	28.5	6.13	6	62	0
lMY, kg	7,120	2,052	378	16,461	1.62
LL, d	327	71.1	26	676	1.62
PP, %	3.57	0.24	2.51	4.78	0
FP, %	4.19	0.42	1.94	7.00	0

[1] iPF = interval from parturition to first service; cPF = potential estrus cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC = potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

[2] Cycles are counted considering cFC = 1 for cows pregnant at first service.

Table 2. Estimates[1] of sire (σ^2_s), herd (σ^2_{he}), permanent environmental cow (σ^2_{pe}), and residual (σ^2_e) variance components of fertility and production traits

Trait[2]	σ^2_s	σ^2_{he}	σ^2_{pe}	σ^2_e
Fertility traits				
iPF, d	1.746 x 10^{1}	2.124 x 10^{2}	1.919 x 10^{2}	9.919 x 10^{2}
cPF, n	2.011 x10^{-2}	1.913 x 10^{-1}	1.670 x 10^{-1}	1.00
NR56	1.049 x 10^{-2}	6.112 x 10^{-2}	5.342 x 10^{-2}	1.00
CFS	1.560 x 10^{-2}	5.153 x 10^{-2}	6.823 x 10^{-2}	1.00
INS, n	1.670 x 10^{-2}	5.146 x 10^{-2}	8.822 x 10^{-2}	1.00
iFC, d	2.737 x 10^{1}	1.286 x 10^{1}	3.395 x 10^{1}	3.138 x 10^{3}
cFC, n	1.589 x 10^{-2}	4.868 x 10^{-2}	9.224 x 10^{-2}	1.00
iPC, d	7.326 x 10^{1}	3.033 x 10^{2}	7.483 x 10^{2}	3.774 x 10^{3}
cPC, n	2.226 x 10^{-2}	8.081 x 10^{-2}	1.512 x 10^{-1}	1.00
Production traits				
pMY, kg	5.286 x 10^{-1}	9.716	4.095	1.292 x 10^{1}
lMY, kg	8.402 x 10^{4}	9.365 x 10^{5}	8.778 x 10^{5}	1.652 x 10^{6}
LL, d	4.779 x 10^{1}	3.837 x 10^{2}	5.043 x 10^{2}	3.427 x 10^{3}
PP, %	4.680 x 10^{-3}	1.644 x 10^{-2}	1.932 x 10^{-2}	1.846 x 10^{-2}
FP, %	1.213 x 10^{-2}	3.200 x 10^{-2}	5.978 x 10^{-2}	6.685 x 10^{-2}

[1] Estimates are the means of the marginal posterior distributions for the variance components.

[2] iPF = interval from parturition to first service; cPF = potential estrus cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC = potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d

after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

Table 3. Estimates[1] of heritability (h^2), intra-herd heritability (h^2_{IH}), herd effect (h^2_{he}), and permanent environmental cow effect (h^2_{pe}) of fertility and production traits

Trait[2]	h^{2} (HPD95%)	h^{2}_{IH} (HPD95%)	h^{2}_{he} (HPD95%)	h^{2}_{pe} (HPD95%)
Fertility traits				
iPF, d	0.049 (0.035; 0.066)	0.058 (0.041; 0.078)	0.150 (0.139; 0.162)	0.136 (0.127; 0.144)
cPF, n	0.058 (0.043; 0.077)	0.068 (0.050; 0.089)	0.139 (0.128; 0.150)	0.121 (0.113; 0.130)
NR56	0.037 (0.027; 0.051)	0.039 (0.028; 0.054)	0.054 (0.048; 0.061)	0.047 (0.035; 0.060)
CFS	0.055 (0.040; 0.073)	0.058 (0.042; 0.077)	0.045 (0.040; 0.052)	0.060 (0.048; 0.072)
INS, n	0.058 (0.043; 0.076)	0.060 (0.045; 0.080)	0.044 (0.039; 0.050)	0.076 (0.065; 0.088)
iFC, d	0.030 (0.020; 0.043)	0.031 (0.021; 0.044)	0.035 (0.031; 0.040)	0.093 (0.083; 0.104)
cFC, n	0.055 (0.041; 0.072)	0.057 (0.042; 0.075)	0.042 (0.037; 0.048)	0.080 (0.069; 0.091)
iPC, d	0.060 (0.044; 0.080)	0.064 (0.074; 0.085)	0.062 (0.055; 0.069)	0.153 (0.142; 0.163)
cPC, n	0.071 (0.053; 0.092)	0.076 (0.057; 0.099)	0.064 (0.058; 0.071)	0.120 (0.111; 0.130)
Production traits				
pMY, kg	0.078 (0.061; 0.097)	0.121 (0.095; 0.150)	0.356 (0.340; 0.374)	0.150 (0.143; 0.158)
lMY, kg	0.095 (0.074; 0.118)	0.129 (0.101; 0.160)	0.264 (0.249; 0.279)	0.247 (0.238; 0.256)
LL, d	0.044 (0.031; 0.059)	0.048 (0.034; 0.065)	0.088 (0.080; 0.096)	0.116 (0.106; 0.125)
PP, %	0.318 (0.269; 0.372)	0.441 (0.376; 0.513)	0.279 (0.263; 0.295)	0.328 (0.318; 0.339)
FP, %	0.284 (0.238; 0.334)	0.349 (0.294; 0.410)	0.187 (0.175; 0.201)	0.350 (0.340; 0.360)

[1] Estimates are the means (HPD95%) of the marginal posterior distributions for the parameters.

[2] iPF = interval from parturition to first service; cPF = potential cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC

= potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

Table 4. Estimates[1] of genetic (ρ_g) and phenotypic (ρ_p) correlations between fertility traits

Trait[2]	cPF		cFC		cPC		INS	
	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p
iPF	0.97 $^{(0.96; 0.98)}$	0.99 $^{(0.99; 0.99)}$	0.46 $^{(0.27; 0.63)}$	-0.07 $^{(-0.08; -0.06)}$	0.81 $^{(0.73; 0.87)}$	0.65 $^{(0.65; 0.66)}$	0.30 $^{(0.09; 0.49)}$	-0.10 $^{(-0.12; -0.09)}$
iFC	0.46 $^{(0.26; 0.63)}$	-0.07 $^{(-0.80; -0.06)}$	0.85 $^{(0.77; 0.90)}$	0.87 $^{(0.86; 0.87)}$	0.83 $^{(0.75; 0.89)}$	0.79 $^{(0.79; 0.79)}$	0.67 $^{(0.53; 0.78)}$	0.85 $^{(0.85; 0.85)}$
iPC	0.75 $^{(0.65; 0.83)}$	0.48 $^{(0.47; 0.49)}$	0.78 $^{(0.69; 0.86)}$	0.78 $^{(0.78; 0.79)}$	0.96 $^{(0.94; 0.97)}$	0.95 $^{(0.94; 0.95)}$	0.76 $^{(0.66; 0.83)}$	0.75 $^{(0.74; 0.75)}$
cPF			0.38 $^{(0.18; 0.54)}$	-0.07 $^{(-0.08; -0.06)}$	0.74 $^{(0.65; 0.82)}$	0.64 $^{(0.63; 0.65)}$		
cFC					0.76 $^{(0.66; 0.83)}$	0.75 $^{(0.74; 0.75)}$		
INS	0.24 $^{(0.03; 0.43)}$	-0.10 $^{(-0.11; -0.09)}$	0.82 $^{(0.74; 0.88)}$	0.78 $^{(0.78; 0.79)}$	0.66 $^{(0.53; 0.76)}$	0.68 $^{(0.67; 0.68)}$		
CFS	-0.33 $^{(-0.51; -0.13)}$	0.04 $^{(0.03; 0.05)}$	-0.77$^{(-0.85; -0.67)}$	-0.68 $^{(-0.69; -0.67)}$	-0.64 $^{(-0.75; -0.61)}$	-0.61 $^{(-0.62; -0.61)}$	-0.78 $^{(-0.85; -0.68)}$	-0.73 $^{(-0.74; -0.73)}$
NR56	0.20$^{(-0.03; 0.41)}$	0.13 $^{(0.12; 0.14)}$	-0.37 $^{(-0.56; -0.16)}$	-0.48 $^{(-0.49; -0.48)}$	-0.07$^{(-0.29; 0.16)}$	-0.32 $^{(-0.33; -0.31)}$	-0.46 $^{(-0.63; -0.26)}$	-0.57 $^{(-0.58; -0.56)}$

[1] Estimates are the means (HPD95%) of the marginal posterior distributions for the correlation.

[2] iPF = interval from parturition to first service; iFC = interval from first service to conception; iPC = interval from parturition to conception; cPF = potential estrus cycles from 21 d after parturition to first service; cFC = potential estrus cycles from first service to conception; cPC = potential estrus cycles from 21 d after parturition to conception; INS = number of inseminations to conception; CFS = conception rate at first service; NR56 = non-return rate at 56 d post-first service.

Table 5. Estimates[1] of genetic (ρ_g) and phenotypic (ρ_p) correlations between production and categorical fertility traits

Trait[2]	cPF		cFC		cPC		INS	
	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p
pMY, kg	$0.38^{(0.21; 0.53)}$	$-0.01^{(0.00; 0.00)}$	$0.28^{(0.08; 0.46)}$	$0.05^{(0.04; 0.07)}$	$0.35^{(0.18; 0.51)}$	$0.02^{(0.00; 0.03)}$	$0.24^{(0.04; 0.42)}$	$0.07^{(0.05; 0.08)}$
lMY, kg	$0.56^{(0.42; 0.68)}$	$0.22^{(0.20; 0.23)}$	$0.39^{(0.21; 0.55)}$	$0.35^{(0.34; 0.37)}$	$0.56^{(0.43; 0.68)}$	$0.43^{(0.41; 0.44)}$	$0.34^{(0.16; 0.51)}$	$0.35^{(0.33; 0.36)}$
LL, d	$0.64^{(0.50; 0.75)}$	$0.37^{(0.36; 0.38)}$	$0.61^{(0.45; 0.74)}$	$0.50^{(0.49; 0.51)}$	$0.76^{(0.66; 0.84)}$	$0.66^{(0.66; 0.67)}$	$0.54^{(0.36; 0.69)}$	$0.45^{(0.44; 0.46)}$
PP, %	$-0.23^{(-0.38; -0.06)}$	$-0.01^{(-0.02; 0.01)}$	$-0.18^{(-0.36; 0.00)}$	$0.12^{(0.10; 0.13)}$	$-0.26^{(-0.41; -0.10)}$	$0.07^{(0.06; 0.09)}$	$-0.14^{(-0.32; 0.05)}$	$0.13^{(0.11; 0.14)}$
FP, %	$-0.03^{(-0.20; 0.13)}$	$0.02^{(0.00; 0.03)}$	$-0.07^{(-0.25; 0.12)}$	$0.05^{(0.03; 0.06)}$	$-0.06^{(-0.22; 0.11)}$	$0.04^{(0.03; 0.05)}$	$-0.08^{(-0.25; 0.11)}$	$0.04^{(0.03; 0.05)}$

[1] Estimates are the means (HPD95%) of the marginal posterior distributions for the correlation.

[2] pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage; cPF = potential estrus cycles from 21 d after parturition to first service; cFC = potential estrus cycles from first service to conception; cPC = potential estrus cycles from 21 d after parturition to conception; INS = number of inseminations to conception.

Figure 1.

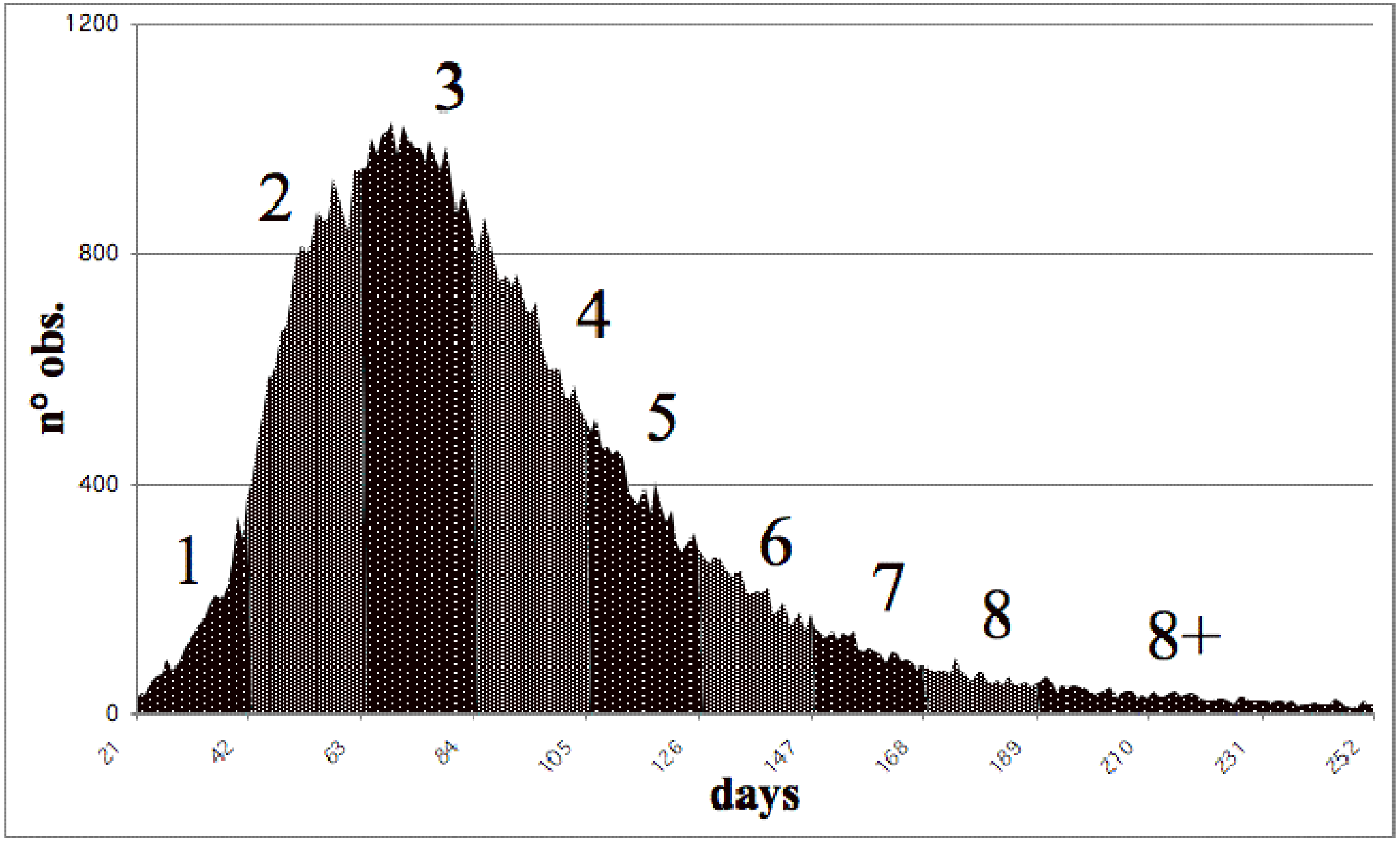

Figure 1. Distribution of records across days from 21 d after parturition to first service. Different colors are intervals of 21 d.

Figure 2.

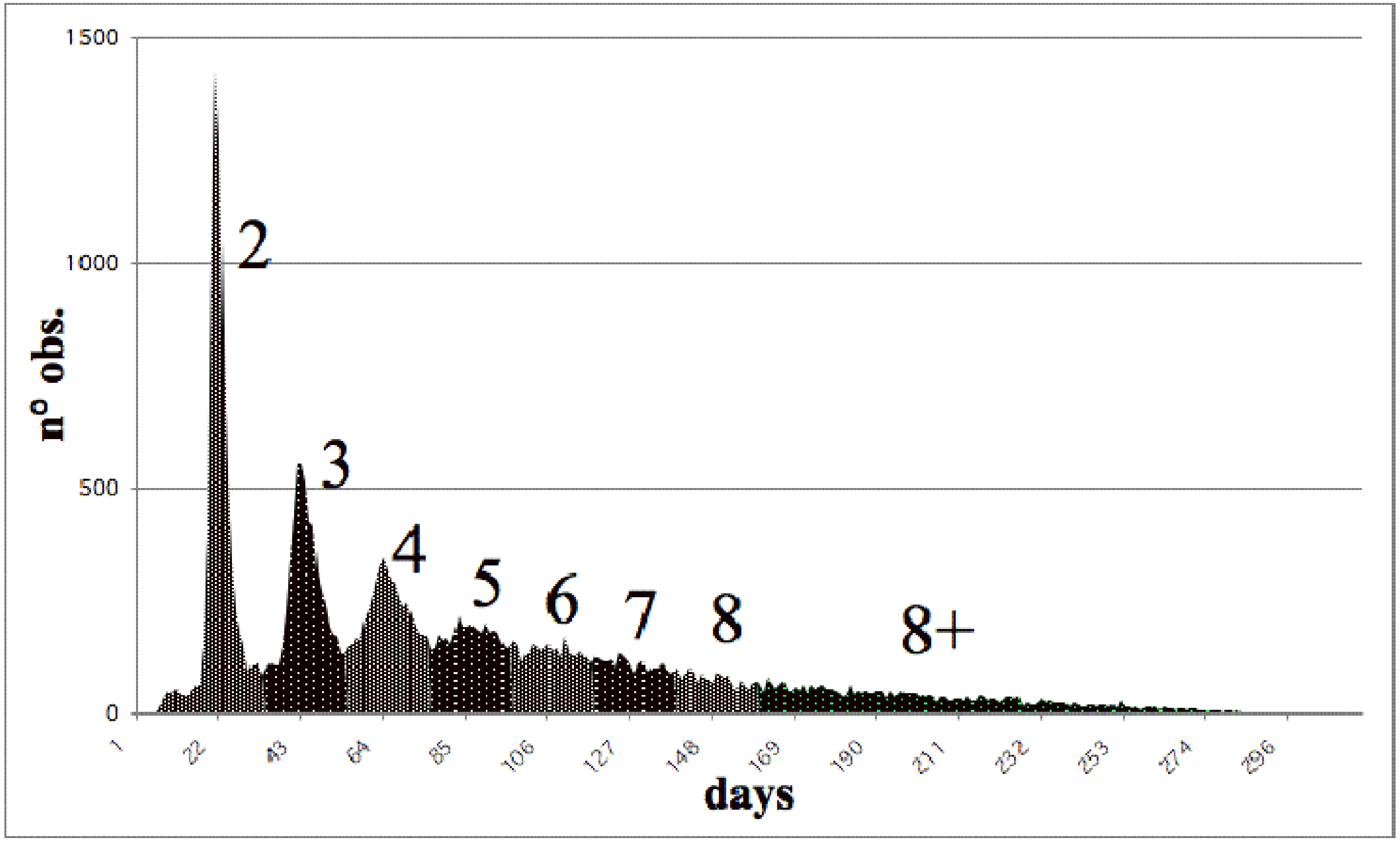

Figure 2. Distribution of records across days from first service to conception. Different colors are intervals of 21 d; interval 1 (0 d, cows pregnant at first insemination) has been voluntary omitted due to high frequency (n = 39,732).

Figure 3.

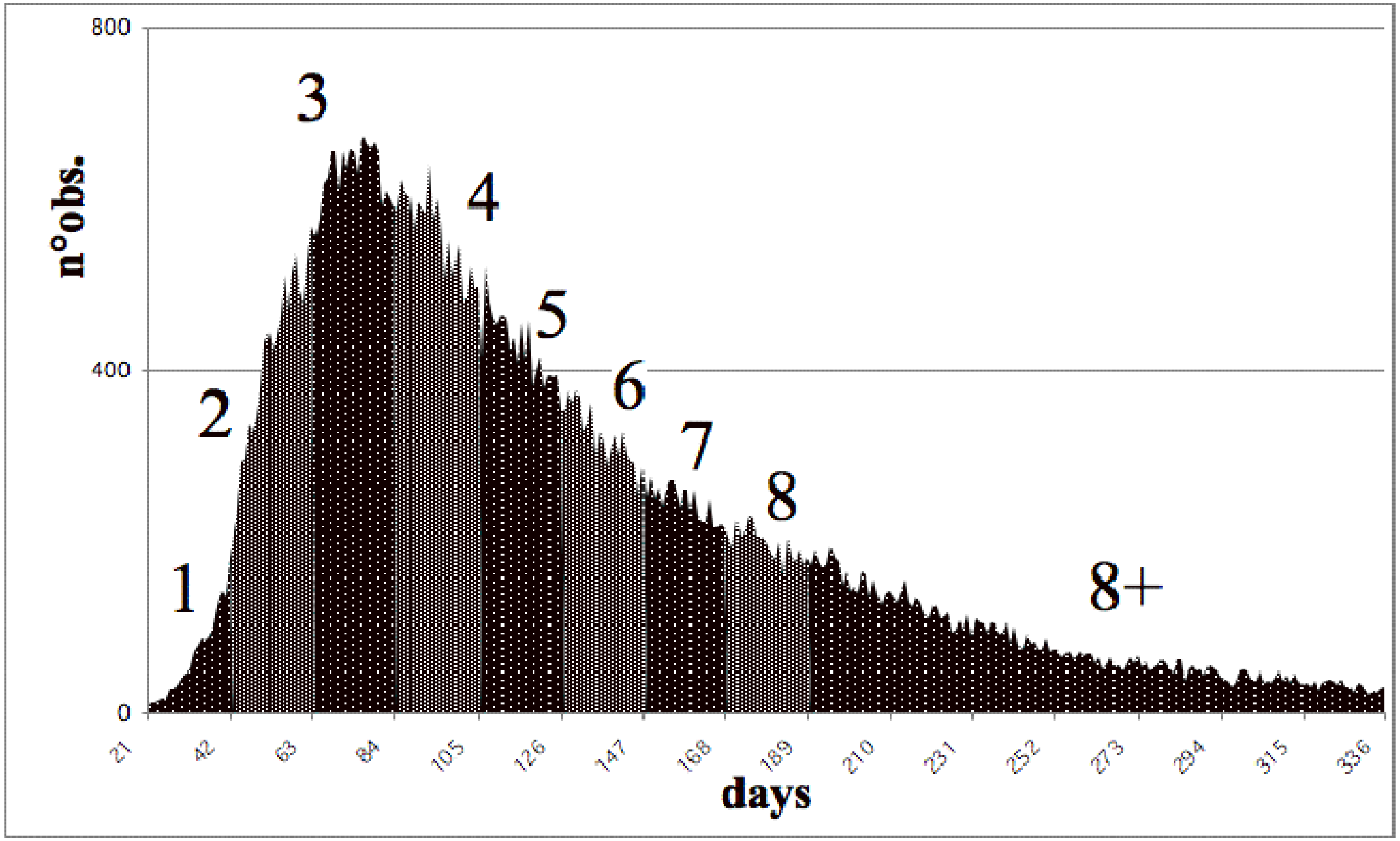

Figure 3. Distribution of records across days from 21 d after parturition to conception. Different colors are classes of 21 d.

Chapter four

Genetic parameters of fertility and production traits for the Italian Brown Swiss population at different parities

Introduction

Female fertility has become a major breeding goal in the dairy cattle industry. In the last decades, different measures of reproductive fitness have been included in several merit indexes worldwide (Van Raden et al., 2004; Andersen-Ramberg et al., 2005; Miglior et al., 2005). When a fertility measure is available, it is possible to evaluate it as the same trait across parities of a given animal (Berry et al., 2003; González-Recio et al., 2006; König et al., 2008) or as a different trait according to the parity considered (Hansen et al., 1983; De Jong, 1998; Andersen-Ranberg et al., 2005). In the latter approach, a possible difference in the physiological status of a virgin heifer compared with a lactating cow is assumed, and the factors affecting fertility are supposed to be of different magnitude across the lactations. Here, the heterogeneity of variances can lead to different heritability estimates for the same trait recorded on different parities, and to non-one genetic correlations across parities. From a genetic point of view, given a pool of genes affecting the overall fertility of an individual, the expression of the genes on the virgin heifer might be significantly different to the expression on a lactating cow; and again, in a first-parity cow, which did not complete her growth at calving, the genes expression and the physiological status may be not equal on later parities, as pluriparous cows could have lost her body reserves (de Jong, 1998).

Several studies showed differences in variance components across parities. Although the estimates of heritability found across parities did not differ significantly (Muir et al., 2004; Holtsmark et al., 2008; Zink et al., 2011), Mantysaari and Van Vleck (1989), Raheja (1989a) and Oltenacu et al. (1991) found that the genetic correlation for the same fertility trait on virgin heifers and first lactation cows was approximately zero. Anyway, Hodel et al. (1995), Muir et al. (2004) and Andersen-Ranberg et al. (2005) found the same genetic correlation to be medium to low, and Jamrozik et al. (2005), Gredler et al. (2007), Holtsmark et al. (2008) and Liu et al. (2008) found medium to high genetic correlations.

The genetic antagonism between fertility and simultaneous production is well known. However, heifer fertility has been demonstrated to be weakly related to production at first parity. Hansen et al. (1983) and Oltenacu et al. (1991) found genetic correlation between heifer fertility and first parity milk yield to be not significantly different from zero. Mantysaari and Van Vleck (1989) found that the same genetic correlation with milk yield was zero for heifer fertility, but moderate for first parity fertility, whereas Hodel et al. (1995) reported a larger difference between the correlations of the heifers and primiparous cows. Similarly, Andersen-Ranberg et al. (2005) and Holtsmark et al. (2008) estimated a moderate genetic correlation between first parity fertility and first lactation protein yield, but it was null if heifer fertility was considered. However, Muir et al. (2004) reported heifer fertility to be more strongly related to production than first parity fertility did. From a practical point of view, the choice of considering a fertility measure as the same or as a different trait across the parity of an animal for its inclusion in merit index is not trivial. Heifer traits are definitely earlier-recording, and offer an evaluation of fertility unbiased by milk yield. On the other hand, lactating cow fertility is the trait which mostly suffered a loss (Andersen-Ranberg et al., 2005), and reflects the real ability of a cow to conceive when milk yield hampers reproductive physiology.

The aim of this study is to estimate genetic parameters of fertility in the Italian Brown Swiss population, considering the reproductive measures in different parities as different traits and to estimate the relationship between fertility and production traits.

Materials and Methods

Data Collection and Editing Procedure

Insemination and production records on Brown Swiss cows were obtained from the Breeders Association of Bolzano-Bozen Province (Italy), as previously reported by Tiezzi et al. (2011). Data were from individuals calving from 1999 to 2007 and progeny of 527 AI bulls. Animals having records in a given parity were required to show records in all the previous parities (heifer status included). Fertility measures were available for virgin heifers (n = 37,546), and first (n = 24,098) and second (n = 15,653) parity cows reared on 2,035 herds. In addition, we considered production traits from first-parity cows, which were peak milk yield (**pMY**, kg), lactation milk yield (**lMY**, kg) and lactation length (**LL**, d). Fertility traits were interval from parturition to first service (iPF), interval from first service to conception (iFC), interval from parturition to conception (iPC), number of inseminations to conception (INS), conception at first service (CFS) and non-return at 56days after first service (NR56) for first and second parity cows. For virgin heifers, the same traits considered except for iPF and iPC. Traits iPF, iFC, and iPC were edited as follows: between 21 and 400 d for iPF and iPC, and between 0 and 400 d for iFC. Traits iFC and iPC were considered censored if a subsequent calving was not recorded. all interval traits were treated as linear Gaussian variables. INS was coded as an ordinal categorical variable according to the number of services needed to achieve pregnancy, and inseminations occurring within 6 days were considered as a single service. The variable consisted of five classes. An arbitrary penalty of 1 insemination was added to records which missed subsequent calving, in an approach similar to the one used by Hou et al. (2009) for days open. Conception rate at first service and NR56 were coded as dichotomous variables according to the achievement of pregnancy at first service for CFS, or the occurrence of a second breeding within 56 d after first service (0) or not (1) for NR56.

Herds with less than 3 first lactation cows were discarded as well as cows that moved to a different herd during the specific period considered. Sires were required to have a minimum of 5 observations (daughters) with first parity records, distributed across at least 3 herds.

Statistical analysis

Univariate censored linear, and threshold analyses were performed for Gaussian and categorical variables, respectively, according to the following models:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Z_h h} + \mathbf{Z_{ss} ss} + \mathbf{Z_t t} + \mathbf{Z_s s} + \mathbf{e}$$

and

$$\boldsymbol{\lambda} = \mathbf{X\beta} + \mathbf{Z_h h} + \mathbf{Z_{ss} ss} + \mathbf{Z_t t} + \mathbf{Z_s s} + \mathbf{e}$$

where $\mathbf{y_i}$ is the vector of observations for linear traits; $\boldsymbol{\lambda}$ is the vector of unobserved liabilities for the categorical traits; $\boldsymbol{\beta}$ is the vector of systematic effects (specific to each class of traits); **h** is the vector of random effects for herds; **ss** is the vector of random effects for service sires (only for CFS and NR56), **t** is the vector of technician random effect (only for CFS and NR56), **s** is the vector of random genetic effect for sires of cows; and **X**, $\mathbf{Z}_{\mathrm{h}}$, $\mathbf{Z}_{\mathrm{ss}}$, $\mathbf{Z}_{\mathrm{t}}$, and $\mathbf{Z}_{\mathrm{s}}$ are incidence matrices relating the corresponding effects to the dependent variable. Fixed effects were: year-month of first calving for pMY, lMY, and LL; year-month of calving of the respective parity for iPF and iPC; the respective year-month of first insemination for iFC, INS, CFS and NR56.

Censored records were handled via data augmentation (Tanner and Wong, 1987; Guo et al., 2001;), so that the linear model for censored records became:

$$\mathrm{y_c} \sim \mathrm{N}(\mathbf{X\beta} + \mathbf{Z_{h,c} h} + \mathbf{Z_{s,c} s}, \sigma^2_c)\ \mathrm{I}(y_c,\infty)$$

where $\mathrm{y_c}$ is the value (augmented over the observed) assumed for every censored record and I is an indicator variable which assumes value 1 if the record is censored, 0 otherwise. In this situation, censored records are augmented over the observed according to the variance components estimated on the previous iterations, and being right censored, the simulated value falls between the observed (y_c) and ∞. For categorical variables with multinomial sampling the probability function was:

$$\mathrm{Prob}(y_i = j|\, \beta,\mathbf{h},\mathbf{s},\mathbf{T}) = \Phi[\mathrm{T_j} - (\mathbf{X}\ \boldsymbol{\beta} + \mathbf{Z_{h,i}\ h} + \mathbf{Z_{s,i}\ s})] - \Phi\ [\mathrm{T_{j\text{-}1}} - (\mathbf{X}\ \boldsymbol{\beta} + \mathbf{Z_{h,i}\ h} + \mathbf{Z_{s,i}\ s})]$$

where j is the threshold to which the observation belongs, $\Phi(.)$ is the standard cumulative normal distribution function, and T are the unknown thresholds assumed as ordinal categorical variables, so that $-\infty = \mathrm{T_0} \leq \mathrm{T_1} \leq \mathrm{T_2} \leq \mathrm{T_j} = \infty$. The unobserved liability for the $\mathrm{y_i}$=j observation falls between the thresholds j and the threshold j-1; thresholds are sampled at every iteration. Having a single threshold for binary variables, that was fixed to ‘0’.

Bivariate analyses were carried out to investigate the genetic relationship among fertility traits considered different traits on the different parities and between fertility and production traits. (Co)variance components were obtained fitting linear-linear, threshold-linear, and threshold-threshold sire models. Systematic and random effects were identical to the univariate analyses. Gibbs sampling was implemented in a Bayesian framework. Bounded uniform priors were used for all systematic effects, and null means and normal univariate or bivariate prior distributions for sire ($\boldsymbol{s} \sim N(0, \mathbf{S_0} \otimes \mathbf{A})$), herd ($\boldsymbol{h} \sim N(0, \mathbf{H_0} \otimes \mathbf{I})$), service sire ($\boldsymbol{ss} \sim N(0, \mathbf{SS_0} \otimes \mathbf{I})$), and technician ($\boldsymbol{t} \sim N(0, \mathbf{T_0} \otimes \mathbf{I})$) random effects were assumed, similarly to the previous contribution ($\mathbf{S_0}$ is the sire covariance matrix, $\mathbf{A}$ is the relationship matrix, $\mathbf{H_0}$ is the herd covariance matrix, $\mathbf{SS_0}$ is the service sire covariance matrix, $\mathbf{T_0}$ is the technician covariance matrix, $\mathbf{I}$ is an identity matrix).

Residuals for linear traits were assumed correlated and normally distributed, $\boldsymbol{e} \sim N(0, \mathbf{R_0} \otimes \mathbf{I})$, R_0 being the residual (co)variance matrix, although residual variances were forced to 1 in case of threshold analysis.

For univariate models a single Gibbs chain of 250,000 samples was obtained, while for bivariate models 550,000 iterations were run. In all the cases the first 50,000 samples were discarded as burn-in. Samples were stored every 20 iterations for univariate models and 50 iterations for bivariate models. The posterior mean was used as a point estimate of the (co)variance component and the related parameter. Lower and upper bounds of the 95% highest posterior probability density regions for heritabilities and additive genetic correlations were calculated from the Gibbs samples.

Heritability was computed as:

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_h^2 + \sigma^2{}_{ss} + \sigma_t^2 + \sigma_e^2}$$

and genetic correlations were calculated as:

$$\rho_g = \frac{\mathrm{cov}_s(x, y)}{\sigma_{s,x}\sigma_{s,y}}$$

Results and Discussion

Descriptive statistics

Descriptive statistics for fertility and productive traits are in Table 1. Mean values for fertility traits common to the three parities showed better results for virgin than first and second parity cows; INS increased from 1.56 of heifers to 1.75 and 1.72 of first and second parity cows, respectively. The same happened for CFS (0.65 *vs* 0.55 and 0.56) and NR56 (0.79 *vs* 0.71), whereas iFC showed only a limited increase (35.6 *vs* 38.3 and 36.3). Traits iPF and iPC did not show any difference between first and second lactation (90.7 *vs* 90.3 for iPF; 129 *vs* 126 for iPC). Approximately 12% of the cows having heifer records did not exhibited a recorded first calving on a national basis, and the same happened for more than 13% of first lactation cows (which did not show second calving) and 17% of second lactation cows (which did not show third parity). These records were considered censored for iFC, iPC and INS. While iFC and iPC were handled via data augmentation, for INS a penalty was added to the recorded number of inseminations if subsequent parity resulted missing or more than 4 services were performed. Table 1 reports the descriptive statistics for INS after penalty adding indicated with INS*. Lactation milk yield averaged 6,794 kg, and was similar to the value reported for the Italian Brown Swiss cattle population based on all available test-day records (AIA, 2010).

Heritability and genetic correlations among fertility traits

Heritabilities of fertility traits are in Table 2. The four fertility traits common to all parities (iFC, INS, CFS, NR56) showed the lowest heritability values on heifers, whereas estimates for first and second parity cows were higher and comparable (0.017-0.039-0.029 for iFC; 0.026-0.046-0.045 for INS; 0.020-0.030-0.032 for CFS; 0.016-0.017-0.026 for NR56). Heritabilities for iPF and iPC were higher for first than second parity cows (0.142 *vs* 0.115 and 0.093 *vs* 0.050, respectively). Hodel et al. (1995), using data from Swiss Simmental cattle, reported higher estimates of heritability for non-return at 90 days in first lactation cows than heifers (1.1% vs 2.1% on the observed scale, 2.0% vs 3.4% on the liability scale), and Jamrozik et al. (2005), in Canadian Holstein cattle, estimated heritabilities of 2.9 and 4% for non-return rate at 56 d in lactating heifers, and second and later parities, respectively, 2.9 and 6.9% for the number of services to conception, and 3 and 7% for the days between first service to conception. Anyway, Muir et al. (2004), Andersen-Ranberg et al. (2005), Gredler et al. (2007), Holtsmark et al. (2008) and Liu et al. (2008) did not find any significant difference in heritability between heifers and first lactation cows. Comparing estimates of heritability for reproductive traits in first and second parity cows, neither

Mitchell et al. (2005) on US Holsteins, and Raheja et al. (1989b) on Canadian Holsteins found significant differences.

Genetic correlations assessed by treating reproductive performance over parities as different traits are in Table 2. The highest estimates were obtained between first and second parity cows; values were ways higher than 0.95, except for INS (0.925). Genetic correlations between heifers and first parity cows were of medium to low magnitude, and were around 50% for iFC and INS, and 35% for CFS and NR56. For the latter two traits, the zero was included within the 95% highest probability interval. Again, binary variables resulted in lower values of genetic correlation than linear and multinomial categorical variables. Our result for the genetic correlations between heifers and first lactation cows for iFC is close to findings of Liu et al. (2008) on German Holstein (0.48), higher than the value by Hodel et al. (1995) on Swiss Simmental (0.37), and lower than the value by Jamrozik et al. (2005) on Canadian Holstein (0.76) cattle. For INS, Jamrozik et al. (2005) estimated a genetic correlation of 0.74 between heifers and first lactation animals, whereas the value assessed on German and Austrian Simmental by Gredler et al. (2007) was 0.68. Both studies applied linear models for the analyses of INS, whereas our finding (0.510) was obtained by using a threshold model. For NR56, Muir et al. (2004) estimated a genetic correlation of 0.22 on Canadian Holstein using a linear model, whereas the value assessed using a threshold analysis by Holtsmark et al. (2008) on Norwegian Red was notably higher (0.61). Andersen-Ranberg et al. (2005), Gredler et al. (2007), and Liu et al. (2008) found values higher than 50% with linear models. Genetic correlations between heifers and second lactation cows ranged from 60 to 70%, being in the midway of genetic correlations between heifers and first parity cows, and first and second parity cows.

Relationships between fertility and production traits

Heritabilities for production traits were 0.130 (0.099 to 0.166) for pMY, 0.118 (0.089 to 0.153) for aMY, and 0.052 (0.032 to 0.077) for LL (results not shown). Genetic correlations between production aspects measured on first lactation cows and fertility traits measured on heifers, and first and second parity cows are in Table 3. Correlations between production and reproductive traits in first parity cows followed the pattern of a recent study by Tiezzi et al. (2011) on the same population; pMY showed medium correlation with iPF, meaning that higher producing cows have delayed first estrous, and low correlations with other fertility traits. Lactation milk yield is more strongly related to contemporary fertility than pMY, and LL is the productive trait mostly correlated to fertility, being lactation elongation a consequence of low fertility.

Heifer fertility is not genetically correlated to production of first parity cows, indicating that cows are not predisposed to be unfertile genetically, but it is likely milk yield to depress fertility. This is in agreement with Hodel et al. (1995) who found production in first lactation Swiss Simmental cows to be more strongly related to contemporary fertility than heifer measures (0.24 *vs* 0.69 for interval between first and last service; -0.21 *vs* -0.58 for non-return at 90 days). On Norwegian Red cows, considering protein yield at 305 days of lactation as production trait, Andersen-Ranberg et al. (2005) and Holtsmark et al. (2008), reported genetic correlations for heifer and first parity fertility of 0.04 *vs* -0.18 and -0.07 *vs* -0.24, respectively.

Production of first lactation animals is even strongly related to second parity fertility, although the relationship is not as strong as with the simultaneous fertility. The metabolic impact of duration of lactation and dry period may be reflected on subsequent fertility, as LL is the most related trait.

Conclusions

The present study demonstrated that although it might be unconcerned to measure fertility in first or second lactation, heifer fertility cannot be considered a good predictor of cow fertility. High genetic correlations were found between first and second parity fertility, whereas genetic correlations between heifer fertility and fertility of lactating cows were moderate. If the genetic evaluation for female fertility is established on heifer data, it should be taken into account that the genetic progress on lactation cows will be smaller than expected. Results suggest that the metabolic demand to support milk yield may lead to scarce reproductive performance, which is not shown on non-lactating heifers. Moreover, reproductive performance in heifers is not supposed to suffer from selection for milk yield, as lactating cow would likely do. Genetic correlations between first parity yield and heifer fertility found in the present study are approximately zero, thus heifer fertility and production do not appear to be genetically related.

Table 13. Descriptive statistics for production and reproductive traits over parities

Trait[1]	Mean	SD	Min	Max	% censored
Heifer fertility traits (n=37,546)					
iFC	35.6	71.5	0	400	12.08
INS[2]	1.56	0.92	1	5	12.47
INS[3]	1.73	1.02	1	5	0[3]
CFS	0.65	0.48	0	1	0
NR56	0.79	0.41	0	1	0
First parity fertility traits (n=24,098)					
iPF	90.7	41.9	21	392	0
iFC	38.3	60.4	0	348	13.29
iPC	129	71.4	21	400	13.29
INS[2]	1.75	1.04	1	5	14.24
INS[3]	1.93	1.12	1	5	0[3]
CFS	0.55	0.50	0	1	0
NR56	0.71	0.46	0	1	0
Second parity fertility traits (n=15,653)					
iPF	90.3	41.0	21	398	0
iFC	36.3	57.7	0	351	17.17
iPC	126	67.9	22	399	17.17
INS[2]	1.72	1.02	1	5	17.86
INS[3]	1.94	1.12	1	5	0[3]
CFS	0.56	0.50	0	1	0
NR56	0.71	0.45	0	1	0
First parity productive traits (n=24,098)					
pMY	25.3	4.52	6	50	0
lMY	6,794	1,892	378	14,455	1.23
LL	336	74.2	45	639	1.23

[1] iPF = interval between parturition and first service; iFC = interval between first service and conception; iPC = interval between parturition and conception; INS = number of inseminations to conception; CFS = conception at first service; NR56 = non-return rate at 56 days from first service; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length.

[2] actual number of inseminations to conception.

[3] values taken into account in computations for number of inseminations to conception (INS) after 1-service penalty adding for non-re-calving cows.

Table 2. Heritabilities for reproductive traits on heifers, first parity and second parity cows, and genetic correlations between the reproductive traits measured on different parities

	Heritability			Genetic correlation		
	Heifers	1st parity	2nd parity	Heifers/1st	1st/2nd	Heifers/2nd
iPF	-	$0.142^{(0.098 \text{ to } 0.195)}$	$0.115^{(0.066 \text{ to } 0.177)}$	-	$0.984^{(0.941 \text{ to } 0.999)}$	-
iFC	$0.017^{(0.009 \text{ to } 0.029)}$	$0.039^{(0.022 \text{ to } 0.061)}$	$0.029^{(0.013 \text{ to } 0.051)}$	$0.551^{(0.261 \text{ to } 0.773)}$	$0.964^{(0.837 \text{ to } 0.999)}$	$0.709^{(0.408 \text{ to } 0.919)}$
iPC	-	$0.093^{(0.062 \text{ to } 0.132)}$	$0.050^{(0.026 \text{ to } 0.084)}$	-	$0.985^{(0.934 \text{ to } 0.999)}$	-
INS	$0.026^{(0.015 \text{ to } 0.041)}$	$0.046^{(0.027 \text{ to } 0.071)}$	$0.045^{(0.023 \text{ to } 0.075)}$	$0.510^{(0.210 \text{ to } 0.741)}$	$0.925^{(0.689 \text{ to } 0.998)}$	$0.646^{(0.360 \text{ to } 0.850)}$
CFS	$0.020^{(0.009 \text{ to } 0.037)}$	$0.030^{(0.013 \text{ to } 0.054)}$	$0.032^{(0.012 \text{ to } 0.061)}$	$0.348^{(-0.124 \text{ to } 0.733)}$	$0.967^{(0.813 \text{ to } 0.999)}$	$0.637^{(0.217 \text{ to } 0.940)}$
NR56	$0.016^{(0.005 \text{ to } 0.032)}$	$0.017^{(0.003 \text{ to } 0.037)}$	$0.026^{(0.006 \text{ to } 0.055)}$	$0.349^{(-0.113 \text{ to } 0.738)}$	$0.965^{(0.825 \text{ to } 0.999)}$	$0.636^{(0.212 \text{ to } 0.946)}$

[1] iPF = interval between parturition and first service; iFC = interval between first service and conception; iPC = interval between parturition and conception; INS = number of inseminations to conception; CFS = conception at first service; NR56 = non-return rate at 56 days from first service; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length.

Table 3. Genetic correlations between production traits measured on first lactation cows and reproductive traits measured on heifers, first parity, and second parity cows

	Peak milk yield			Lactation milk yield			Lactation lenght		
Trait	Heifers	1st parity	2nd parity	Heifers	1st parity	2nd parity	Heifers	1st parity	2nd parity
iPF	-	0.414 (0.214 to 0.593)	0.353 (0.117 to 0.561)	-	0.617 (0.450 to 0.753)	0.465 (0.234 to 0.662)	-	0.877 (0.776 to 0.944)	0.798 (0.583 to 0.952)
iFC	-0.128 (-0.415 to 0.160)	0.214 (-0.045 to 0.464)	0.293 (-0.046 to 0.598)	-0.083 (-0.369 to 0.203)	0.493 (0.268 to 0.682)	0.487 (0.178 to 0.753)	0.251 (-0.092 to 0.556)	0.895 (0.791 to 0.962)	0.794 (0.519 to 0.975)
iPC	-	0.275 (0.054 to 0.488)	0.295 (0.007 to 0.560)	-	0.510 (0.310 to 0.675)	0.400 (0.129 to 0.657)	-	0.933 (0.858 to 0.982)	0.865 (0.643 to 0.997)
INS	-0.099 (-0.362 to 0.164)	0.204 (-0.066 to 0.458)	0.249 (-0.070 to 0.550)	-0.023 (-0.295 to 0.242)	0.472 (0.235 to 0.674)	0.428 (0.130 to 0.691)	0.213 (-0.101 to 0.49)	0.810 (0.639 to 0.927)	0.616 (0.300 to 0.859)
NR56	0.019 (-0.361 to 0.420)	-0.250 (-0.710 to 0.213)	-0.230 (-0.600 to 0.238)	-0.187 (-0.522 to 0.207)	-0.439 (-0.902 to -0.007)	-0.286 (-0.684 to 0.132)	-0.081 (-0.494 to 0.403)	-0.467 (-0.923 to 0.020)	-0.140 (-0.621 to 0.359)
CFS	0.000 (-0.333 to 0.340)	-0.142 (-0.482 to 0.190)	-0.281 (-0.642 to 0.115)	-0.153 (-0.460 to 0.18)	-0.553 (-0.800 to -0.251)	-0.514 (-0.819 to -0.156)	-0.215 (-0.565 to 0.186)	-0.822 (-0.991 to -0.583)	-0.657 (-0.930 to -0.286)

[1] iPF = interval between parturition and first service; iFC = interval between first service and conception; iPC = interval between parturition and conception; INS = number of inseminations to conception; CFS = conception at first service; NR56 = non-return rate at 56 days from first service; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length.

Chapter five

The genetic relationship between fertility, production, and body condition score in Italian Brown Swiss.

Introduction

The genetic evaluation for female fertility in dairy cattle relies on direct measures of fertility parameters (Gredler et al., 2007; Miglior, 2007; Nilforooshan et al., 2010), or correlated traits, such as angularity (Biffani et al., 2005), milk urea nitrogen (Mitchell et al., 2005) and body condition score (Dal Zotto et al., 2007). Body condition score (BCS) is considered a management tool, perhaps subjective, able to denote both energy status and body fat reserves in cattle (Edmonson et al., 1989). Just the ratio of fat to non-fat components in the body of a live animal (Murray, 1919) is the element to be assessed through visual and tactile appraisal, thus transformed in scoring.

In the past years BCS has been expressed in 4 points (Lowman et al., 1973) 5 points (Wildman et al., 1982; Edmonson et al., 1989), 6 points (Mulvaney, 1977), 8 points (Earle, 1976), or 10 points (Roche et al., 2004) scales, but the general rationale is that low values reflect emaciation and high values equate to obesity (Roche et al., 2009).

Dairy cattle BCS is usually classified by trained technicians, and the accuracy and repeatability has been widely studied (Ferguson et al., 1994; Hady et al, 1994; Veerkamp et al., 2002). When BCS measurements were compared intra- and inter-classifier results have been discordant. Edmonson et al. (1989) found good consistency in scoring, as inter-classifier variability was small, and experience did not show any significant effect on classifier's repeatability. Veerkamp et al. (2002) found that genetic correlations between scorings of different classifiers treated as different traits were seldom significantly different from unity, while Kristensen et al. (2006) found that training resulted as a major factor defining repeatability within and across technician.

In high-yielding dairy cattle, constrained feed intake jointly to high milk yield leads to mobilization of adipose tissue reserves in response to the energy deficit, which denotes the pattern of loss (from beginning to mid lactation) and recovery (in late lactation), such that BCS has been found to be a reliable predictor of energy balance (Coffey et al., 2003; Roche et al., 2009; Banos and Coffey, 2010). Moreover, Waltner et al. (1993), Gallo et al. (1996), and Pryce et al. (2001) found this pattern to be different across lactations and productive level, as primiparous cows tended to have slighter loss than second and later parity cows, and high yielding cows had more condition loss than low yielding cows.

Thus, BCS is related to productive and reproductive traits. Several studies (Veerkamp et al., 2001; Pryce et al., 2002; Dal Zotto et al., 2007) reported negative genetic correlation between BCS and milk yield ranging between -0.30 and -0.48, indicating that more productive cows tend to be less conditioned. The same phenotypic correlations were still negative but weaker, probably due to environmental effects mitigating the loss of condition in high yielding cows.

Concerning reproductive traits, body condition loss has been shown to be phenotypically related to bad fertility (Suriyasathaporn et al., 1998; Domecq et al., 1997; Gillund et al., 2001), rather than single BCS measure. Cows showing bad conditioning did not necessary meet bad fertility, but the loss of body condition in early lactation involved low reproductive performance.

On the genetic level, BCS was found to be positively related to good fertility. Using single scoring during lactation, Dal Zotto et al. (2007), Dechow et al. (2004), Pryce et al. (2002), Rossoni et al. (2007b), Zink et al. (2011) found genetic correlations between BCS and fertility measures (calving interval or days from parity to conception) ranging between -0.30 and -0.67, indicating that the genetically less conditioned cows will be likely to take a longer time to conceive after calving.

Several authors used repeated observations during the same lactation, modeling BCS with multiple trait (Dechow et al., 2001; Gallo et al., 2001; Berry et al., 2003) and random regression (Veerkamp et al., 2001; De Haas et al., 2007; Bastin et al., 2010) models. Anyway, genetic correlations appeared to be concordant to those reported above, although of stronger magnitude in early-mid lactation.

BCS could be a predictor of fertility in those dairy cattle populations where direct assessment of reproductive fitness is not included in the total merit index, such as Italian Brown Swiss dairy cattle. As already reported by Dal Zotto et al. (2005, 2007) and Rossoni et al. (2007a, 2007b) since 2002 the Italian Brown Cattle Breeders Association is recording BCS on primiparous cows.

The aim of this work was therefore to investigate the genetic relationship between BCS and fertility parameters, verifying the possibility to use BCS as predictor of female fertility in the Italian Brown Swiss population.

Materials and Methods

Data Collection and Editing Procedure

Body condition measures and pedigree information were provided by the Italian Brown National Breeders Association, insemination and production records were obtained from the Breeders Association of Bolzano-Bozen Province (Italy), the population was already characterized in Tiezzi et al. (2011). Data included 16,324 cows reared in 1,413 herds, animals calved from 2002 to 2007 and were progeny of 420 AI bulls. BCS is routinely measured once in first lactation by trained classifiers according to the method of Edmonson et al. (1989), based on a 5-point scale with 0.25-unit increments, on evaluation of 8 body areas. For this study, BCS measure was required to fall between 10 and 180 days in milk. Classifiers had to show at least 20 measures to be included in the analysis.

First lactation fertility and production records were merged to BCS measurements, second lactation fertility records were merged as well, where available. Production traits considered were peak of lactation milk yield (**pMY**, kg), whole lactation milk yield (**lMY**, kg) and lactation length (**LL**, d). Fertility traits were iPF, iFC, iPC, INS, CFS and NR56 for first and second parity. Traits iPF, iFC, and iPC were edited as follows: between 21 and 400 d for iPF and iPC, between 0 and 400 d for iFC. iFC and iPC were considered censored if a subsequent calving was not recorded. All these, production traits, and BCS were treated as linear Gaussian variables.

INS was coded as an ordinal categorical variable according to the number of services needed to achieve pregnancy, and inseminations occurring within 6 days were considered as a single service. The variable consisted of five classes. An arbitrary penalty of 1 insemination was added to records which missed subsequent calving, in an approach similar to the one used by Hou et al. (2009) for days open. Conception rate at first service and NR56 were coded as dichotomous variables according to the achievement of pregnancy at first service for CFS, or the occurrence of a second breeding within 56 d after first service (0) or not (1) for NR56.

Herds with less than 3 cows were discarded as well as cows that moved to a different herd during the specific period considered. Sires were required to have a minimum of 5 observations (daughters) with first parity records, distributed across at least 3 herds.

Statistical analysis

Univariate censored linear, and threshold analyses were performed for Gaussian and categorical variables, respectively. Methodology involved was identical to that of the previous chapter.

Results and Discussion

Descriptive statistics

In table 1 are reported the descriptive statistics for BCS, milk yield, and reproductive traits. In total 16,324 records for BCS, production and reproduction on first parity were available, while on second parity 10,086 were considered only for fertility traits. BCS averaged 3.16, with a standard deviation of 0.32, ranging between 1.75 and 4.75. This is in accordance with data reported by Dal Zotto et al. (2007) from a related Italian Brown Swiss population, where BCS averaged 3.20

with a 0.35 standard deviation. Means and standard deviations for fertility and productive traits are close to values reported in previous studies on the same population (Tiezzi et al., 2011).

Heritability and genetic correlations among BCS and fertility and productive traits.

Heritabilities for BCS, productive and fertility traits are reported in table 2. Heritability for BCS was 0.127 (with 95% from 0.089 to 0.174), which is lower than values found by other authors in Italian Brown Swiss. Dal Zotto et al. (2005, 2007) found 0.178 and 0.15 heritability values, respectively, and Rossoni et al. (2007a) found 0.19 heritability. Other authors found higher h^2 estimates than present with single measurements of BCS during lactation. Zink et al. (2011) in Czech Holstein found a 0.3 heritability for BCS measured on a 9 point scale, Dechow et al. (2004) reported 0.22 on US Holstein, while Pryce et al. (2002) found 0.39 on UK Holstein.

The reduced size of the dataset did not alter significantly heritability estimates for production and fertility traits compared to previous studies (Tiezzi et al., 2011).

Other random effects included in the model for BCS, such as herd and classifier, accounted for 7% (5.7% to 9% HPD intervals) and 23% (13% to 38% HPD intervals) of total variance. While herd appeared not relevant in determining cow condition, classifier effect showed the largest magnitude. Quantifying the variation due to the classifier random effect cannot be considered a robust measure of repeatability and consistency of this effect, as cows were scored only once by a single technician. Anyway, given the large variation among the score of the classifiers, a classifier effect is recommended to be taken into account when estimating genetic parameters.

Phenotypic and genetic and correlations between BCS and other traits are also reported in table 2. On the phenotypic level BCS resulted to be not significantly correlated to milk yield or reproductive fitness, as all the correlations were below 10% as absolute value. This is somehow in accordance to Suriyasathaporn et al. (1998), Domecq et al. (1997), Gillund et al. (2001), and Dechow et al. (2004), who found single measures of BCS not to be phenotypically related to reproductive fitness.

BCS resulted to be moderately related to contemporary fertility, genetic correlations ranged between -0.280 with INS and 0.496 with NR. Anyway, for all the fertility traits less than 10% of the samples resulted to be different from 0 or of an opposite sign respective to sign of the mean. Thus, BCS measured once per lactation may be not a good predictor of contemporary fertility. Actually, both on Brown Swiss and Holstein several authors found stronger genetic correlations between fertility and BCS. On Brown Swiss, relating BCS to calving interval, Rossoni et al. (2007b) found -0.67 and Dal Zotto et al. (2007) found -0.35.

On Holstein, BCS was related as -0.48 with CI (Pryce et al., 2002), as -0.30 with days open (Dechow et al., 2004), and as -0.30 with IFC, -0.46 with IPC,and -0.45 with IPF (Zink et al., 2011).

Anyway, in the present study, BCS was strongly genetically related to pMY (-0.556), aMY (-0.533), and LL (-0.341). This is accordance with the studies reported above.

Second parity interval fertility traits were surprisingly more related to BCS than contemporary fertility did, but success traits were still less related. Here, interval fertility traits showed means of the marginal posterior densities lower than -0.3 and less than 5% of the samples were of positive sign. Succes fertility trait had a weaker correlation to BCS, mostly for CFS and NR. A possible explanation is that measuring BCS once per lactation cannot express the real energy deficit of the cow, which properly leads to low fertility. Otherwise, a general low conditioning in the previous lactation could exploit its effect on delaying first estrous or hampering pregnancy establishment. In a similar study, Zink et al. (2011), found similar genetic correlations between first lactation BCS and second lactation IPC and IPF, and lower correlation with IFC.

Conclusions

The present study examined genetic aspect of body conditions score in relation to yield and fertility. Body condition scores were assessed once during first lactation. Production appeared to be strongly related to body conditions, as more productive cows were more likely to be less conditioned. Fertility was considered both as simultaneous, i. e. measured in first lactation, and consecutive, thus measured in second lactation. Results revealed that contemporary fertility was poorly related to body condition, but results are not too far from those reported in literature on single BCS measures. Consecutive fertility was moderately linked to body condition.

The present study suggests in Italian Brown Swiss the variation in body condition imputable to additive genetic effect is small, and genetic correlations with fertility are moderate. This may suggest that in this breed low BCS does not mean scarce reproductive performance.

Anyway, further studies investigating the scoring at different point in lactation and condition loss are needed.

Table 1: Descriptive statistics for body condition score (BCS), first lactation milk yield, and first and second parity fertility traits.

Trait[1]	**Mean**	**SD**	**Min**	**Max**	**% censored**
First Parity Fertility and Body Condition Score, n = 16,324					
BCS	3.16	0.32	1.75	4.75	0.00
IPF	90.7	41.9	21	392	0.00
IFC	38.8	60.9	0	348	13.2
IPC	129.5	71.6	21	400	13.2
INS	1.76	1.05	1	5	14.3
CFS	0.55	0.50	0	1	0.00
NR	0.71	0.46	0	1	0.00
First Parity Milk Yield, n = 16,324					
PMY	25.7	4.51	8	50	0.00
AMY	6,972	1,902	700	14,455	1.02
ALL	338	73.9	45	639	1.02
Second Parity Fertility, n = 10,086					
IPF	90.8	41.5	21	398	0.00
IFC	36.9	58.4	0	351	17.6
IPC	127.6	68.7	23	399	17.6
INS	1.74	1.04	1	5	18.4
CFS	0.56	0.50	0	1	0.00
NR	0.71	0.46	0	1	0.00

[1] BCS = body condition score measured once in first lactation; iPF = interval between parturition and first service; iFC = interval between first service and conception; iPC = interval between parturition and conception; INS = number of inseminations to conception; CFS = conception at first service; NR56 = non-return rate at 56 days for first service; pMY = lactation peak milk yield; lMY = lactation milk yield; LL = lactation length.

Table 2: Estimates[1] of heritability, and genetic and phenotypic correlations for body condition score (BCS), first lactation milk yield, and first and second parity fertility traits.

Trait[1]	**h^2**	**Genetic correlation with BCS**	**Phenotypic correlation with BCS**
Body Condition Score			
BCS	$0.127^{(0.089 \text{ to } 0.174)}$	.	.
First Parity Fertility			
IPF	$0.063^{(0.037 \text{ to } 0.097)}$	$-0.225^{(93)}$	$-0.098^{(100)}$
IFC	$0.053^{(0.029 \text{ to } 0.085)}$	$-0.210^{(90)}$	$-0.030^{(100)}$
IPC	$0.088^{(0.054 \text{ to } 0.131)}$	$-0.172^{(89)}$	$-0.070^{(100)}$
INS	$0.064^{(0.036 \text{ to } 0.100)}$	$-0.280^{(97)}$	$-0.025^{(100)}$
CFS	$0.044^{(0.019 \text{ to } 0.079)}$	$0.300^{(95)}$	$0.015^{(93)}$
NR	$0.019^{(0.003 \text{ to } 0.044)}$	$0.496^{(98)}$	$0.005^{(66)}$
First Parity Milk Yield			
PMY	$0.137^{(0.100 \text{ to } 0.182)}$	$-0.556^{(100)}$	$0.060^{(100)}$
AMY	$0.099^{(0.067 \text{ to } 0.138)}$	$-0.533^{(100)}$	$0.038^{(100)}$
ALL	$0.047^{(0.026 \text{ to } 0.075)}$	$-0.341^{(99)}$	$-0.041^{(100)}$
Second Parity Fertility			
IPF	$0.180^{(0.099 \text{ to } 0.277)}$	$-0.291^{(98)}$	$-0.057^{(100)}$
IFC	$0.038^{(0.017 \text{ to } 0.068)}$	$-0.391^{(98)}$	$-0.001^{(56)}$
IPC	$0.071^{(0.035 \text{ to } 0.122)}$	$-0.330^{(97)}$	$-0.026^{(99)}$
INS	$0.057^{(0.028 \text{ to } 0.095)}$	$-0.283^{(94)}$	$-0.000^{(50)}$
CFS	$0.046^{(0.017 \text{ to } 0.087)}$	$0.247^{(88)}$	$0.000^{(50)}$
NR	$0.032^{(0.007 \text{ to } 0.070)}$	$0.123^{(67)}$	$-0.014^{(83)}$

[1] Estimates are the means (lower and upper bound of the 95% highest posterior density region, HPD95%) of the marginal posterior distributions for heritability, and means (with the probability of having samples of sign concordant with the mean) for the genetic and phenotypic correlations.

[2] BCS = body condition score measured once in first lactation; iPF = interval between parturition and first service; iFC = interval between first service and conception; iPC = interval between parturition and conception; INS = number of inseminations to conception; CFS = conception at first service; NR56 = non-return rate at 56 days for first service; pMY = lactation peak milk yield; lMY = lactation milk yield; LL = lactation length.

Chapter six

General conclusions

The present thesis carried out different studies on the various aspects of fertility in dairy cattle. The population study was the Italian Brown Swiss reared in the province of Bolzano. Both male and female fertility were investigated.

For male fertility, results showed that additive genetic variation exists, among service sires, in determining the success of an insemination. Non-return rate at 56 days and conception rate results to be hetiable, although their heritabilities were rarely over 0.1. In the cross validation scheme, where the EBVs different models were assumed to be a predictor, conception rate resulted to be clearly more predictable than non-raturn rate, and this is in accordance with the additive variance component and heritability found. Male fertility can be then predicted, though accuracy remains low.

Different aspects and concerns were covered in the female fertility analysis.

In the first step we defined interval and success traits, which were considered homogeneous across parities. Variance components and heritabilities were calculated for these traits. In addition, interval traits were divided in classes of 21 days period (simulating estrous cycles). Genetic correlations between fertility and production traits were computed. Results showed that additive genetic variation for fertility traits is low but exists, and cycle-measured intervals were perhaps more heritable than days measures interval traits. Anyway, genetic correlations between production and fertility were antagonistic, confirming results found in literature.

Second step was to consider fertility measures as different traits if taken over the different parities. We defined heifer fertility traits, first parity fertility traits, and second parity fertility traits. In addition, first lactation milk yield was considered. Within-parity heritabilities and genetic correlations for the same trait over the different parity were computed. Results showed that, while first parity fertility can be considered equivalent to second parity fertility, heifer fertility should be considered separately. Moreover, first and second lactation fertility measures report the antagonistic correlation found in the previous chapter, but heifer fertility was not correlated to first lactation yield.

Third step aim to investigate the relationship between fertility and body condition score, which is considered the most promising predictor of dairy cattle female fertility. Body condition condition score is currently assessed within the first six months of first lactation. Contemporary fertility and milk yield, and subsequent (second parity) fertility were related to the condition score. Heritability for body condition score was low, and classifier effect adsorbed the most of the variance for this trait. Genetic correlations showed a medium-strong negative relationship with milk yiled, a moderate correlation with the most of contemporary fertility traits. For interval fertility traits, body condition score was more related to subsequent than contemporary fertility, suggesting hte strong carry-over effect that condition score exploit on subsequent lactation.

In conclusion, selection for female fertility seems to be possible. Although low, additive genetic variation exists, and it can lead to moderate response to selection is fertility breeding value is considered in total merit index for dairy cattle. The choice of the trait should be accurate, because earlier recording traits, such as heifer traits, could not give the expected gain in lactating cow reproductive fitness, which is the trait to be rather preserved. Given the antagonistic relationship with production traits, the aim of considering breeding value for fertility is mostly to limit the deterioration fo fertility on the genetic level, than to improve it. Assessing condition score of lactating cows may alleviate the high costs of insemination events collection, although repeated measurements of cow condition on the same lactation would be preferred.

Male fertility should be considered separately. As there is not concern about selection for male fertility on the genetic level, first crop field data can be used to predict the subsequent reproductive fitness of dairy bulls used as service sire.

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