Genetic Parameters and Genetic Trends of Female Fertility in Icelandic Dairy Cattle

Þórdís Þórarinsdóttir

Faculty of Agricultural Sciences
Genetic parameters and genetic trends of female fertility in Icelandic dairy cattle

Þórdís Þórarinsdóttir

60 ECTS thesis submitted in partial fulfilment of a Magister Scientiarum degree in Agricultural Sciences

Academic advisors:
Elsa Albertsdóttir, The Icelandic Agricultural Advisory Centre
Susanne Eriksson, Swedish University of Agricultural Sciences

Faculty supervisor: Emma Eyþórsdóttir

Agricultural University of Iceland
Faculty of Agricultural Sciences
Clarification of contribution

I hereby declare that the writing of this thesis is my work under the supervision of my academic advisors Elsa Albertsdóttir and Susanne Eriksson.

The data for the project came from Huppa, the database and recording program of the Farmers Association of Iceland.

______________________________
Þórdís Þórarinsdóttir
Abstract

Fertility, represented by calving interval, has been included in the genetic evaluation of Icelandic dairy cattle since 1993. In spite of this an unfavourable genetic trend is seen and, recent implementation of test-day models for the genetic evaluation of milk production has changed the premise of using calving interval to represent fertility. The aim of this study was to estimate genetic parameters and genetic trends of different female fertility traits in Icelandic dairy cattle and suggest new traits for the genetic evaluation. Insemination records for the first three lactations and the heifer period of 52,951 Icelandic cows were used to analyse the traits: conception rate at first insemination (CR), number of inseminations per service period (AIS), interval form first to last insemination (IFL), interval from calving to first insemination (ICF), interval from calving to last insemination (ICL) and calving interval (CI). Correlations between fertility and production traits were also estimated. Five different linear animal models were used to estimate (co)variance components. Breeding values were compared, and genetic trends were investigated.

Phenotypic averages of CR and AIS were more favourable for heifers than for cows. Estimated heritabilities for the fertility traits were low in all cases, using both multi-trait models (0.01 – 0.08) and single-trait models (0.02 – 0.06). ICF in second lactation had the highest heritability, and the lowest estimates were found for the heifer traits. Estimated heritabilities of yield traits analysed in the study were in the range from 0.15 to 0.25. Genetic correlations between heifer and cow performances within traits ranged from 0.23 to 0.81. Genetic correlations between lactations within traits ranged from 0.36 to 1.00. Genetic correlations between different heifer traits were strong. Genetic correlations between different fertility traits ranged from weak (-0.17) to very strong (0.97). Genetic correlations between the fertility and production traits were generally unfavourable, but more pronouncedly so for AIS, IFL, ICL and CI than for ICF and CR. Estimated genetic trends seemed unfavourable for the traits AIS, IFL and CI and favourable for ICF and ICL.

Heifer and cow fertility should not be considered as the same trait. Fertility between different lactations should be considered as different but correlated traits. In a revised genetic evaluation for fertility in Icelandic cattle, the traits ICF and IFL should be included to represent cow fertility, and CR to represent heifer fertility. These traits represent the time it takes for the animals to resume the estrous cycle after calving and conceiving once
the insemination period has started. Rank correlations between EBVs suggested there will be some reranking of sires in a new evaluation.

Keywords: Icelandic cattle, fertility, genetic evaluation, genetic trends, genetic correlation, heritability
Ágrip

[Efðaþróun og erfðaþróun frjósemiseiginleika í íslenska kuástofninum]


Meðaltöl svipfarseginleika fanghluftfalla og fjöldu sæðinga voru hagstæðari hjá kvígu en hjá mjólkandi kúm. Arfgengi var lágt fyrr alla frjósemiseiginleikana, bæði þegar notuð voru fjölbreytulíkön (0,01 – 0,08) og likan með einum eiginleika (0,02 – 0,06). Hæsta arfgengi var á eiginleikanum bil milli burðar og fyrstu sæðingar á öðru mjaltaskeiði og lægsta arfgengi var með þyr fyrr kvígu eiginleikana. Arfgengi afurðaeiginleika í rannsókninni voru hærra en fyrr frjósemiseiginleika (0,15 – 0,25). Erfðaþlígni á milli kvigumælinga og mælinga í mjólkandi kúm innan sama eiginleika var á bilinu 0,23 til 0,81. Erfðaþlígni á milli mjaltaskeiðs í nýjan sama eiginleika var á bilinu 0,36 til 1,00. Erfðaþlígni á milli kvingueiginleika vor sterk. Erfðaþlígni á milli mismunandi frjósemiseiginleika var allt frá því að vera veik (-0,17) upp í vera mjög sterk (0,97). Erfðaþlígni vor hófleg en óhagstæð á milli afurðaeiginleika og frjósemiseiginleikanna fjöldi sæðinga, bil milli fyrstu og síðustu sæðingar, bil milli burðar og síðustu sæðingar og bil milli burða. Veikari fylgni var á milli afurða og frjósemiseiginleikanna bil milli burðar og fyrstu sæðingar og fanghluftfalls. Erfðaþróun virtist óhagstæð fyrr eiginleikana fjöldi sæðinga, bil milli fyrstu og síðustu sæðingar og bil milli burða en hagstæð fyrr bil milli burðar og fyrstu sæðingar og bil milli burðar og síðustu sæðingar.

*Lykilorð: Frjósemi, kynbótamat, erfðaframfær, erfðafylgni, arfgengi*
Acknowledgement

Financial support from the Cattle Productivity Fond is acknowledged.

The Farmers Association of Iceland and Guðmundur Jóhannesson are thanked for providing data.

I would like to thank my advisors Elsa Albertdóttir and Susanne Eriksson for their cooperation, valuable advice, guidance and support in the making of this thesis.

Emma Eyþórsdóttir gets my thanks for proofreading and for all her assistance during the project.

My parents Þórarinn Leifsson and Guðrún Lárusdóttir and my fiancé Eyþór Bragi Bragason get my thanks for all their support throughout this project work. Sunna Þórarinsdóttir gets my thanks for proofreading.
## Contents

Clarification of contribution...................................................................................................i 
Abstract ................................................................................................................................. ii 
Ágrip........................................................................................................................................ iv 
Acknowledgement................................................................................................................... vi 

1 Introduction .......................................................................................................................... 1 
1.1 Aims................................................................................................................................... 1 

2 Literature Review .................................................................................................................. 2 
2.1 The Icelandic Dairy Cow..................................................................................................... 2 
2.2 Reproduction in Dairy Cattle............................................................................................ 3 
2.3 Factors that Affect Reproduction ..................................................................................... 4 
  2.3.1 The Estrous Cycle........................................................................................................ 4 
  2.3.2 Postpartum Cyclicity .................................................................................................... 5 
  2.3.3 Estrous Detection........................................................................................................ 6 
  2.3.4 Conception Rate......................................................................................................... 7 
2.4 Decreasing Fertility in Dairy Cattle.................................................................................. 8 
2.5 Breeding Fertile Cows....................................................................................................... 9 
  2.5.1 Genetic Trends............................................................................................................ 10 
  2.5.2 Genomic Selection..................................................................................................... 11 
  2.5.3 Heifer and Cow Fertility........................................................................................... 11 
  2.5.4 Fertility Traits........................................................................................................... 11 
2.6 Fertility in the Icelandic Dairy Cow ................................................................................ 12 
2.7 Genetic Evaluation of Fertility in Other Countries ............................................................ 14 
  2.7.1 The Nordic Dairy Cattle Evaluation......................................................................... 14 
  2.7.2 Norway...................................................................................................................... 15 
  2.7.3 Germany, Austria and Luxemburg.......................................................................... 16 
  2.7.4 United Kingdom........................................................................................................ 16 
  2.7.5 United States of America........................................................................................ 17 
  2.7.6 Canada....................................................................................................................... 17 
2.8 Model Options.................................................................................................................. 17
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Material and Methods</td>
<td>18</td>
</tr>
<tr>
<td>3.1</td>
<td>Data</td>
<td>18</td>
</tr>
<tr>
<td>3.2</td>
<td>Statistical Analysis</td>
<td>20</td>
</tr>
<tr>
<td>4</td>
<td>Results</td>
<td>23</td>
</tr>
<tr>
<td>5</td>
<td>Discussion</td>
<td>32</td>
</tr>
<tr>
<td>5.1</td>
<td>The Fertility Traits on a Phenotypic Level</td>
<td>32</td>
</tr>
<tr>
<td>5.2</td>
<td>Heritability Estimates</td>
<td>33</td>
</tr>
<tr>
<td>5.3</td>
<td>Genetic Correlations</td>
<td>35</td>
</tr>
<tr>
<td>5.3.1</td>
<td>Phenotypic Correlations</td>
<td>35</td>
</tr>
<tr>
<td>5.3.2</td>
<td>Genetic Correlations Between Parities Within Traits</td>
<td>35</td>
</tr>
<tr>
<td>5.3.3</td>
<td>Genetic Correlations Between Fertility Traits</td>
<td>36</td>
</tr>
<tr>
<td>5.3.4</td>
<td>Genetic Correlations Between Fertility Traits and Yield Traits</td>
<td>38</td>
</tr>
<tr>
<td>5.4</td>
<td>Estimated Genetic Trends for Fertility Traits</td>
<td>39</td>
</tr>
<tr>
<td>5.5</td>
<td>New Genetic Evaluation for Fertility</td>
<td>41</td>
</tr>
<tr>
<td>5.5.1</td>
<td>Rank Correlations Between Different Fertility Trait EBVs</td>
<td>43</td>
</tr>
<tr>
<td>6</td>
<td>Conclusion</td>
<td>44</td>
</tr>
<tr>
<td>7</td>
<td>References</td>
<td>45</td>
</tr>
<tr>
<td>8</td>
<td>Appendixes</td>
<td>53</td>
</tr>
<tr>
<td>8.1</td>
<td>Appendix I</td>
<td>53</td>
</tr>
<tr>
<td>8.2</td>
<td>Appendix II</td>
<td>57</td>
</tr>
</tbody>
</table>
List of Tables

Table 1 - Calculation of the NAV fertility index................................................................. 15
Table 2 – Distribution of animals by birth years. ................................................................. 20
Table 3 – Phenotypic averages of female fertility traits in the Icelandic dairy cow................. 23
Table 4 - Variance components\(^a\) of fertility traits using multi-trait models...................... 24
Table 5 - Variance components\(^a\) for fertility traits using single-trait models..................... 25
Table 6 – Genetic correlations\(^a\) between fertility traits in different parities using a multi-trait model (Model 1 and 2). ..................................................................................................................... 26
Table 7 - Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between heifer traits using a three-trait model (Model 2).......................................................... 26
Table 8 - Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between cow traits using a two-trait model (Model 4). .......................................................... 27
Table 9 - Genetic correlations between fertility traits and yield traits using a three-trait model (Model 5). (Phenotypic correlations in parentheses). .......................................................... 28
Table 10 – Spearman rank correlations between EBVs from DMU5 for cows in data with own observations and bulls in pedigree file with 10 or more daughters in the data file of analysed cows. ......................................................................................................................... 31
Table 11 - Heritability estimates for conception rate (CR) in various dairy breeds. ............ 53
Table 12 - Heritability estimates for number of inseminations per service period (AIS) in various dairy breeds. .......................................................................................................................... 53
Table 13 - Heritability estimates for interval from first to last insemination (IFL) in various dairy breeds ........................................................................................................................................ 54
Table 14 - Heritability estimates for interval from calving to first insemination (ICF) in various dairy breeds .......................................................................................................................... 55
Table 15 - Heritability estimates for interval from calving to last insemination (ICL) in various dairy breeds. .......................................................................................................................... 56
Table 16 - Heritability estimates for calving interval (CI) in various dairy breeds................. 56
Table 17 – Phenotypic averages of yield traits used in the study. ........................................... 57
Table 18 - Variance components\(^a\) of yield traits using a single-trait model....................... 58
List of Figures

Figure 1 – Illustration of the fertility traits analysed in the study. ........................................ 19

Figure 2 – Genetic trends (mean EBVs per birth year from DMU5) for animals in the analysed dataset with own observations for the six fertility traits estimated with multi-trait models within each trait (Models 1 and 2) ........................................................................................................... 29

Figure 3 - Genetic trends (mean EBVs per birth year from DMU5) for animals in the analysed dataset using a six-trait model where lactations are repeated measurements..... 30

Figure 4 - Proportion of cows with different number of recorded calvings in the data..... 57
1 Introduction

An essential part of profitable dairy production systems is good reproductive performance. Calving interval has been used as a trait to evaluate female fertility of Icelandic dairy cows since 1993. Even though fertility has been included in the breeding goal, breeding values for fertility have decreased in the last 20 years (Eiríksson & Gautason, 2019). A recent change of the genetic evaluation of milk yield, from lactation yield to test day yield, has changed the premise of using calving interval to evaluate fertility. This is because it now takes much longer to collect information about the calving interval of daughters of AI sires, compared with the collection of production data (Eiríksson et al. 2019a).

Therefore, the feasibility to use other measures of female fertility in a revised genetic evaluation for fertility in Icelandic cattle was investigated in this study.

The analysed female fertility traits were 1) conception rate at first insemination, 2) number of inseminations per service period, 3) interval from first insemination to last insemination, 4) interval from calving to first insemination, 5) interval from calving to last insemination and 6) calving interval.

1.1 Aims

The main aim was to study if the genetic evaluation of Icelandic cattle could be improved by using another trait to represent female fertility. Therefore, the objectives of this project were to:

- Estimate genetic parameters for different female fertility traits in Icelandic dairy cattle.
- Estimate correlations between fertility traits and production traits in Icelandic dairy cattle.
- Investigate genetic trends for fertility traits in Icelandic dairy cattle.
- Suggest new traits for genetic evaluation for fertility in Icelandic dairy cattle.
2 Literature Review

2.1 The Icelandic Dairy Cow

Iceland was colonized in the 9th and 10th century, mainly from Norway. The Icelandic dairy cow is believed to originate from the cows that the first settlers brought with them and is believed to have remained mostly isolated from other cattle populations since then. Genetic studies have indicated that cattle in Iceland are closely related to Norwegian native breeds (Adalsteinsson, 1981; Kantanen, 2000). A recent study by Gautason et al. (2019) showed that Icelandic cattle are genetically distinct from other cattle breeds in Western Europe and they are most related to Northern Nordic indigenous cattle breeds. Icelandic dairy cows are rather small compared to commercial dairy breeds in Europe and America. During the last decades, the breed has grown both in body size and weight, however (Konráðsdóttir, 2010; Sigurðsson, 2017; Sigurdsson & Jonmundsson, 2011).

The Icelandic dairy cow is the only dairy cow breed in Iceland. In December 2019 the number of dairy cows in Iceland was 26,415, whereas the total number of cattle was 81,250 animals (Ráðgjafamiðstöð landbúnaðarins, n.d.-a). In the last two decades, the number of dairy farms in Iceland has decreased, there are more animals per farm, the average yield per cow has increased and the overall milk production has increased. In the year 2000, there were around 1,000 dairy farms in Iceland, the average yield was just under 4,000 kg per cow a year and the total milk production was 104 million litres. In December of 2019, there were 546 dairy farmers in Iceland, the average yield per cow was 6,334 kg and the total milk production in 2019 was 151.8 million litres (Auðhumla, 2020; Gardarsdóttir, 2019; Hagðjónusta Landbúnaðarins, 2010; Ráðgjafamiðstöð landbúnaðarins, 2019).

Milk production in Iceland is in some ways controlled by the government. There are import restrictions and tariffs on milk products to Iceland. There is a knockdown price on milk bound by law to dairy farmers and the wholesale price of several dairy products is also bound by law. Milk is produced within a quota system and farmers who own quota receive a subsidy from the government (Hagfræðistofnun Háskóla Íslands, 2015).

The current breeding program for dairy cattle in Iceland was adopted in the year 1993. The program is based on defined breeding objectives. A BLUP animal model that includes all
known information about the animal and pedigree information is used for genetic evaluation (Ráðgjafamiðstöð landbúnaðarins, n.d.-b; Sigurdsson & Jonmundsson, 2011). A recent report about economic weights of traits in the Icelandic cattle breeding objective led to changes in the breeding goal and the total merit index (TMI). The weight of fertility increased from 8% to 10% for progeny testes bulls and 11% for cows in the revised TMI. The other traits included in the TMI and their new weights (for bulls/ for cows) are: Yield (36/36%), somatic cell score (8/9%), udder (10/11%), teats (10/13%), milking ease (8/10%), temperament (8/10%) and longevity (10/0%) (Eiríksson & Gautason, 2019).

The AI (artificial insemination) bull facility in Iceland is owned by the Farmers Association. Every year they buy selected bull calves from Icelandic farmers. The sires of the calves must be selected bull-sires from the AI station and the mothers must be bull-dams. Semen is collected from the bulls, which is then sold to agriculture societies around the country. Half of the semen doses are from proven bulls and half are from young bulls for progeny testing. The agriculture societies employ AI technicians that visit farmers, and the AI fees differ between areas (Bændasamtök Íslands, n.d.; Eiríksson et al., 2019a; Jóhannesson, 2019, personal communication). SpermVital inseminations became available for use in Iceland on from December 2017 (Jóhannesson, 2018, personal communication). SpermVital is a new insemination technology where sperm cells are immobilized before cryopreservation. This extends the life of spermatozoa after insemination which makes the timing of the insemination less important (SpermVital, n.d.).

2.2 Reproduction in Dairy Cattle

Reproduction has two main functions in dairy cows. The first is to induce the beginning of lactation and the second is to provide replacement animals. Therefore, production and economic efficiency are immensely influenced by reproductive efficiency (Berry et al., 2014; Wathes & Diskin, 2016). Fertility in dairy cows can be described as the ability of the cow to conceive and maintain pregnancy if she is served at the right time relative to ovulation (Lucy, 2019; Pryce et al., 2004).

Many factors like production systems, feed cost, milk production and milk prices influence the optimal reproduction function that maximizes profits. The factors influencing the
reproductive performance of the individual cow, and therefore the herd, generally fall into three categories: 1) Interval from calving until the cow ovulates again and resumes the normal estrous cycle, 2) The efficiency of estrous detection and submission rate, 3) Rate of conception following service (Diskin, 2011).

2.3 Factors that Affect Reproduction

2.3.1 The Estrous Cycle

The estrous cycle enables female animals to go from periods of reproductive receptivity to nonreceptivity and following mating allowing the establishment of pregnancy. In cattle, the estrous cycle is 18-24 days and consists of two phases, the luteal phase and the follicular phase. The period following ovulation is the luteal phase, which is 14-18 days, and that is when the corpus luteum (CL) is formed. After luteolysis (when the CL degenerates), the follicular phase starts. It is 4-6 days and that is when the ovulatory follicle matures and ovulates which leads to the release of an oocyte. The oocyte moves into the oviduct which allows for potential fertilization (Crowe, 2011; Stevenson, 2007).

During a normal estrous cycle, there are generally two or three waves of follicle growth. In each wave a group of follicles grows, a dominant follicle (DF) is selected and then either atresia (follicle breakdown) or ovulation of the DF occurs. It is only in the final wave, that occurs in the follicular phase, where the DF undergoes final maturation, ovulates and becomes the CL of the following luteal phase (Crowe, 2011; Stevenson, 2007).

Numerous hormones control the estrous cycle in cattle: Gonadotropin-releasing hormone (GnRH), luteinizing hormone (LH), follicle-stimulating hormone (FSH), estradiol, progesterone, inhibins and prostaglandin. Insulin-like growth factor I (IGF-I) is also involved (Crowe, 2011; Garverick & Lucy, 2011). A surge in LH in the follicular phase is what causes the DF to ovulate. The CL then secretes progesterone which along with estradiol act as a feedback mechanism to control LH and FSH secretion. In the absence of an embryo, the uterus releases prostaglandin which causes luteolysis of the CL, which then allows the secretion of FSH and LH (Crowe, 2011; Stevenson, 2007).

Heifers reach puberty at the age of 6-24 month and that is when the commencement of the estrous cycle occurs (Crowe, 2011). Body weight and age are the major influences on the
timing of puberty. For economic performance, the optimal age at first calving (AFC) is around 2 years (23-25 months). Heifers must conceive by 15 months of age if this is to be achieved (Wathes et al., 2014; Þórarinsdóttir, 2017).

2.3.2 Postpartum Cyclicity

Cows do not ovulate additional follicles during pregnancy because of the CL. The waves of follicular growth do continue through pregnancy, but the activity decreases as the pregnancy progresses. For a subsequent pregnancy to be established after parturition, ovarian follicular growth and ovulatory follicular cycles must be reinitiated. Factors that affect the fate of postpartum ovarian follicles can be body condition at calving, negative energy balance, and diseases (Crowe, 2011; Garverick & Lucy, 2011; Stevenson, 2007).

A study on the ovarian activity of lactating dairy cows was conducted in Iceland in the years 1983-1986 and 1988-1989. Progesterone measurements were used to estimate the time from calving to the commencement of first postpartum luteal function and to estimate the length of ovarian cycles as well as the length of luteal and follicular phases. The results indicated that the reproductive potential of the Icelandic dairy cows was comparable to that of the main dairy breeds in the U.S.A. and northern Europe (Eldon, 1991).

2.3.2.1 Body Condition and Energy Balance

After parturition, high producing dairy cows experience an increase in energy requirements because of the increase in milk yield. Only a part of the energy requirements can be met by feed consumption, and the cow has to mobilize body reserves which results in a negative energy balance (NEB). It would appear that successful genetic selection for increased milk yield in dairy cattle has exacerbated this problem. For a few weeks after calving, energy and feed intake in lactating cows is not maximized, and during this time the NEB reaches its peak. The severity of the NEB and the body condition of the cow might affect the resumption of postpartum cyclicity (Diskin & Morris, 2008; Garverick & Lucy, 2011; Pryce et al., 2004; Walsh et al., 2011). Cows that are too fat at and following parturition are in a greater NEB than ideally conditioned cows because of decreased appetite after calving. Because of this, they have a much larger decrease in body condition. Conversely, cows in a very poor body condition do not have available energy stores to mobilize for both lactation requirements and maintenance following parturition. The greater the change
in body conditions of the cow after parturition, the longer it takes to resume ovulation. Conception rates are also better in cows with lower NEB then those cows in a higher NEB (Chagas, et al., 2007; Garverick & Lucy, 2011).

When energy conditions do not meet the needs for maternal survival, the body diverts energy away from reproductive processes. Events leading up to the first ovulation begin when the NEB decreases. Pulsatile release and the increasing mean concentration of LH and IGF-I among other things makes the DF ovulate. LH pulsatility decreases with low energy availability and because of this follicular stimulation and estradiol synthesis are less. Cows in a better body condition and a lower NEB show better LH pulsatility (Chagas, et al., 2007; Garverick & Lucy, 2011).

2.3.2.2 Diseases
For cows to have efficient postpartum reproduction, they must be healthy (Garverick & Lucy, 2011; Lucy 2019). The effects of diseases on reproductive performance are larger than of any other factors and diseased cows are less fertile than healthy cows. Negative effects can result from reproductive and metabolic diseases and disorders such as dystocia, retained placenta, milk fever, ketosis and many others. The general health of cows affected by diseases and disorders is usually poorer. They have greater losses in body condition and their postpartum ovarian cyclicity can be delayed. Postpartum reproduction can also be negatively affected by mastitis (Garverick & Lucy, 2011; Walsh et al., 2011).

2.3.3 Estrous Detection
To allow successful mating prior to ovulation, estrous behaviour is closely related to the time of ovulation. This maximizes the chance of conception. Cows will stand to be mounted by herd mates or a bull during estrous. Estrous lasts for 8-24 hours and is expressed at 18-24-day intervals. The cause of the estrous behaviour is the dominant follicle which secretes estradiol before ovulation (Crowe, 2011; O’Connor, 2007). Insufficient circulating estradiol during the preovulatory period may be the reason for lactating cows having a poor estrous expression or fail to express estrous (Lucy, 2019).

The most important factor for heat detection efficiency is the ability of those responsible for checking if the cows are in heat to understand the signs of heat. This is the case if
artificial insemination (AI) is used. In the majority of cases where heat detection fails, management problems are to blame (Diskin, 2011; O’Connor, 2007). An Icelandic study about the benefits of using support equipment for estrous detection suggested clear benefits of e.g. shorter calving interval. In the study, there was better fertility in cows on dairy farms where cows were housed in free stall barns and milked in a milking parlour, than on farms where cows were in free stall barns but milked with an automatic milking robot (Samúelsson, 2015). In 2017 almost 70% of Icelandic cows were in free stall barns and around 45% of Icelandic cows were milked with an automatic milking robot (Sigurðsson, 2018).

2.3.4 Conception Rate

As previously mentioned, the conception rate following service is the third major factor that affects reproductive efficiency. Factors that can cause conception failure or death of the embryo can be physiological, genetic, endocrine or environmental (Diskin, 2011; Wathes, 2016). Many factors do affect the actual pregnancy rate. They mostly relate to the cow itself and the issues can be broadly categorised as related to: 1) energy balance and nutrition, 2) problems at calving and postpartum diseases, 3) seasonal heat stress, 4) insemination technique and bull fertility, 5) genetics and 6) progesterone profile (Wathes, 2016).

Embryonic mortality is one of the main causes of failure in reproduction. The causes of very early embryo mortality (days 0-7) can be an inability of the embryo to develop because of poor quality of the oocyte or because of the inadequate environment in the uterus (Lucy, 2019; Walsh et al., 2011). The growth of the developing embryo can be impaired because of a low concentration of progesterone. High feed intake and the high metabolic state that is required to support lactation is associated with rapid degradation and clearance of steroid hormones in the liver. Circulating progesterone concentration is reduced by steroid clearance. An embryo that is not developed enough may not manage to signal its mother. This might lead to early embryonic death because the pregnancy is not recognized by the uterus. It has been suggested that up to 25% of conception failures in dairy cows are because of failure of maternal recognition of pregnancy and early embryo loss (Lucy, 2019; Walsh et al., 2011).
About 10% of cows pregnant on day 32 will lose their pregnancies before day 60. Scarring and inflammation within the uterus that arises from postpartum uterine infections may be the cause. This affects the ability of the embryo to develop during the second month of pregnancy (Lucy 2019).

2.3.4.1 Important Factors in Establishing Pregnancy
There are several factors of importance for a pregnancy to be established in the dairy heifer or cow (Crowe, 2011; Garverick & Lucy, 2011; Lucy, 2019; Walsh et al., 2011):

1. After parturition: Minimise the loss of body condition score. Resolve post-partum uterine infections.
2. Day 0 of the estrous cycle: Heat detection and insemination of the cow at the correct time.
3. Day 1: The cow must ovulate a high-quality oocyte that is fertilized.
4. Days 3-7: Increase in progesterone secretion.
6. Day 14-18: A large enough embryo to signal the pregnancy.

2.4 Decreasing Fertility in Dairy Cattle
In the last few decades, genetic selection and improved management have caused the average milk yield per cow to increase. The heritability for milk production is moderate, whereas it is low for fertility traits. In addition, the genetic correlation between fertility and milk production is unfavourable. Therefore, there has been a decline in reproductive performance in dairy cows, at least in part because of insufficient consideration of fertility traits when selecting for higher milk production (Berry et al., 2014; Walsh et al., 2011; Wathes, 2016). However, unsuitable management of high producing dairy cows, in addition to direct genetic effects, may contribute to the cause of poor fertility (Rodney et al., 2018; Walsh et al., 2011). Fertility and reproduction problems are among the most common reasons for culling in dairy production (Berglund, 2008; Eriksson, 2017). In 2001, infertility was the reason for 9.6% of culling in Icelandic dairy cows (Jónmundsson, 2002) and in 2016 infertility was the reason for 13% of culling of dairy cows and 32% of culling of heifers in Iceland (G. Jóhannesson, 2017, unpublished material).
As has been stated above, fertility is a multi-factorial trait. The decline in fertility in dairy cows has been caused by a network of factors that are genetic, environmental or management related. Between them are complex interactions, so it can be difficult to determine the exact reason for declining fertility. It is crucial to understand genotype by environment interactions to determine the best health and management practises in order to achieve high reproductive efficiency and high levels of production (Pryce, et al., 2004; Rodney et al., 2018; Walsh et al., 2011).

2.5 Breeding Fertile Cows

In recent years emphasis has shifted in many countries to include more functional traits in bull selection indices. The aim is to breed healthier cows with improved longevity. Declining fertility in dairy cows has altered breeding goals in the direction of those adopted in the Nordic countries as early as the 1960s. This change has helped to stabilize the fertility situation. However, it remains a major challenge to dairy producers to maintain cow health and fertility and milk yield at the same time. Female fertility is now a standard component in breeding programs for modern dairy cattle. There is no perfect way to measure or describe fertility as is it affected by many factors. It is therefore a complex breeding goal compared to production traits (Berry et al., 2014; Muuttoranta et al., 2019; Philipsson & Lindhé, 2003; Walsh et al., 2011; Wathes, 2016).

All fertility traits have low heritability, usually less than 5%, and to enhance genetic gain they therefore have to be assigned a significant weight in breeding programs. The reason for the low heritability is the large influence of management and environmental effects on fertility and reproduction (Berglund, 2008; Berry et al., 2014; Muuttoranta et al., 2019). Another issue is that female fertility traits often include censored observations, e.g. when cows are culled with unknown pregnancy status, mistakes in recording or because data were collected when a record was still in progress (Liu et al., 2017; Muuttoranta et al., 2019).

Accurate modelling of fertility traits is crucial, and it is important to account for correlations between different fertility traits to capture the numerous aspects of fertility (Berglund, 2008; Muuttoranta et al., 2019). Even though fertility traits have relatively low
heritabilities, their additive genetic variances have remained adequately high so effective selection can be performed (Liu et al., 2017).

2.5.1 Genetic Trends

In the worldwide spread Holstein breed, the genetic trend for fertility had been shown to be unfavourable (Philipsson & Lindhé, 2003). Genetic merit for calving interval (CI) in Irish Holstein-Friesian dairy cows increased (i.e. worsened) between the years 1980-2004 when breeding objectives were entirely based on milk production. After 2005, CI began to decrease again (i.e. improved). Similarly, in the UK, genetic merit for CI in Holstein-Friesian decreased until 2009, where after it started to improve. In Australian Holstein-Friesian, CI deteriorated until 2005, and then it started to improve. Many other dairy populations show similar genetic trends in reproductive performance as a consequence of changed breeding goals (Berry et al., 2014).

In Sweden, the increasing use of imported Holstein genetics previously caused a decline in fertility in Swedish Holstein even though reproductive performance has been included in the breeding goal and the selection criteria for many years in the Nordic countries (Berglund, 2008; Muuttoranta et al., 2019). The inclusion of fertility in the Swedish breeding goal was not enough to withstand the import of genetic material from countries that had either no weighing of fertility in the breeding objective or low weighing. The Swedish Red breed, which has similar milk yield levels and genetic trend in yield, had meanwhile largely maintained fertility (Berglund, 2008).

More recently genetic trends have indicated an improvement for some fertility traits since many countries started to define more comprehensive breeding goals in their selection (Philipsson, 2011). In a study by Tyrisevä et al. (2017), it was shown that the genetic trend of conception rate (CR) was improving in the Nordic countries. This applied to all breeds, Holstein, Red dairy cattle and Jersey, and all parities (Tyrisevä et al., 2017). In a study by García-Ruiz et al. (2016) genetic trends for fertility had rapidly improved since genomic selection (GS) in dairy cattle was implemented in the United States of America in 2008.
2.5.2 Genomic Selection

A genomic evaluation has been implemented in many countries, e.g. in the United States, Canada and the Scandinavian countries (Weller et al., 2017). Genomic selection (GS) was first described by Meuwissen et al. (2001) but it became a reality later when high-density SNP (single-nucleotide polymorphism) arrays became commercially available (Berry et al., 2014). GS has a large effect on how reliable breeding values of animals without own record or progeny are. In addition, GS shortens generation intervals. GS along with other breeding tools can help accelerate improvement in low heritability traits like fertility traits and reproduction (Berry et al., 2014; García-Ruiz et al., 2016). The Farmers Association of Iceland in collaboration with other organizations are in the process of implementing GS in Iceland (Gautason, 2018).

2.5.3 Heifer and Cow Fertility

Generally, fertility in maiden heifers is better than in lactating cows (Liu et al., 2017; Walsh et al., 2011). Fertility data from heifers become available for analysis earlier in the animals’ lives and describes reproductive performance that is not biased by milk production. However, the fertility of lactating cows shows their ability to conceive when they are under the metabolic load of lactating and as previously discussed, this trait was previously declining (Berglund, 2008; Berry et al., 2014; Tiezzy et al. 2012).

Studies have shown that genetic correlations between fertility traits in maiden heifers and lactating cows can vary from low to high. A correlation below one suggests that the genetic control of fertility traits is different at least to some degree in heifers and lactating cows. This should be taken into account when breeding programs are designed. An explanation for this might be that the metabolic load is greater in lactating cows than in maiden heifers (de Haer et al., 2013; Muuttoranta et al., 2019; Pryce et al., 2004; Tiezzy et al., 2012).

2.5.4 Fertility Traits

The challenge of breeding for fertility is the collection of data as well as the quality of the data. Generally, fertility traits are based on calving and insemination data, and each trait has its weaknesses and strengths (Berglund, 2008). Management has a significant influence on fertility traits. This is because estrous has to be detected and insemination time
determined (Hoekstra et al., 1994). The fertility traits used in the international genetic
evaluation of dairy sires are grouped into five categories (Interbull, 2019a):

(T1) The ability of a maiden heifer to conceive.
(T2) The ability of a lactating cow to resume cyclicity after calving.
(T3) The ability of a lactating cow to conceive expressed as a rate trait.
(T4) The ability of a lactating cow to conceive expressed as an interval trait.
(T5) Lactating cow’s measurements of the interval trait calving to conception

Traits that can be used to measure fertility are: Interval from calving to first insemination
in days (ICF), interval from first to last insemination in days (IFL), interval from calving to
last insemination in days/days open (ICL/DO), conception rate (CR), number of
inseminations per service period (AIS), calving interval in days (CI), age at first
insemination (AFI) and nonreturn rate (NRR, no return to service within a set time period
after insemination) (Eriksson et al., 2017; de Haer et al., 2013; Muuttoranta et al., 2019).
These traits can be divided into categories as interval traits (ICF, IFL, ICL/DO, CI, AFI),
binary traits (NRR and CR) and count traits (AIS). All those measures depend on the data
recorded to be reliable. The traits ICF and CI are the most common ones used to evaluate
fertility in dairy cattle. In dairy cow fertility studies, the interval traits tend to have greater
heritability than the binary traits and the count traits (Berry et al., 2014; Pryce et al., 2004).
Heritability estimates for various dairy breeds can be seen in Tables 11-16 in Appendix I
where they range from 0.008 to 0.142.

2.6 Fertility in the Icelandic Dairy Cow

Fertility has been included in the total merit index for Icelandic cattle since 1993. In the
years 1993-2005 fertility weighed 4% in the index but in 2005 the weight was increased to
8%. Breeding values for fertility in Icelandic cattle have decreased in the last 10 years, and
the weight was therefore increased to 10% for progeny tested bulls and 11% for cows in
the total merit index in 2019 (Eiríksson & Gautason, 2019; Sigurdsson & Jonmundsson,
2011).

In Icelandic dairy cattle, calving interval (CI) has been used as a fertility measure since
1993 (Sigurdsson & Jonmundsson, 2011). CI captures the cow’s ability to recommence
normal cyclicity after parturition, express estrous intense enough to be detected and to

12
conceive and establish pregnancy (Berry et al., 2014). The strength of CI is that two
calving dates are an obvious measurement much less affected by the quality of data than
other fertility measures. The weakness of CI as a fertility trait is that the cow has to calve
twice for information to be collected. Information about CI is not available for cows that
are culled before subsequent calving. This might lead to overestimation of reproductive
efficiency (Tiezzy et al., 2011). When breeding values for fertility are estimated in
Icelandic dairy cattle, a multi-trait animal model is used where the first three lactations are
considered as separate traits. Fixed effects in the model are herd × calving year(s), month
of calving and age at calving (Sigurðsson, 2007).

In 2018 the Icelandic breeding program was changed when a test day model for milk yield
replaced lactation yield in the evaluation (Ráðgjafamiðstöð landbúnaðarins, n.d.-b). The
advantage of the test day model is that proven AI bulls can be chosen earlier because their
daughters are no longer required to milk a whole lactation and calve again before their
record can be used in the analyses. However, this changes the premise for the selection of
other traits, especially fertility. Daughters of an AI sire must calve (at least) twice to get a
fertility record in the current system, and therefore fertility information for genetic
evaluation is delayed compared to production records. This, along with the low heritability
of CI, makes the fertility evaluation of the bulls unreliable at the time when they are
selected. To counteract this, different methods of evaluating fertility can be used, e.g. by
using insemination data and different fertility traits (Eiríksson et al. 2019a; Eiríksson, n.d.).

Use of natural service (NS) bulls is rather extensive in Iceland (Sigurdsson &
Jonmundsson, 2011). In a report on insemination fees from 2018 it was estimated that in
2017, 78% of cows and 66% of maiden heifers were inseminated with AI bulls
(Jóhannesson, 2018). According to results from the recording system of Icelandic cattle in
2019, only 69% of born calves were sired by AI bulls (Ráðgjafamiðstöð landbúnaðarins,
2019). The use of NS bulls has been reported to slow down genetic progress and has a
negative effect on the economic return from milk production in Iceland (Kristófersson &
Jónmundsson, 2006; Sigurdsson & Jonmundsson, 2011). Heavy use of NS bulls can cause
problems when analysing AI data e.g. because of data censoring.

A recent study by Gautason et al. (2019) showed the effective population size of Icelandic
cattle to be 71 which is quite low, and the study concluded that genomic inbreeding trends
need to be carefully supervised. Excessive inbreeding can lead to a decrease in
performance e.g. of fertility (Bourdon, 2000) which quite clearly shows the need to be
cautious in the future breeding work of Icelandic cattle, especially regarding the
implementation of genomic selection.

2.7 Genetic Evaluation of Fertility in Other Countries

In this literature review, emphasis will be put on fertility evaluations in Scandinavia. Traits
used in some other countries will also be mentioned.

2.7.1 The Nordic Dairy Cattle Evaluation

The Nordic countries Denmark, Finland and Sweden carry out a joint genetic evaluation
for dairy cattle. The Nordic Dairy Cattle Evaluation (NAV) was established in 2002 and
calculates the breeding values for Holstein, Red Dairy cattle and Jersey. All economically
important traits are included in an index, the Nordic Total Merit index (NTM). The traits in
the NTM are weighted based on their economic value and they are adjusted according to
future predictions of the economic situation for the dairy sector (NAV Nordic Cattle
Genetic Evaluation, 2019a, 2019b). The changes in the economic value of fertility in the
NTM are mostly due to changes in calving interval. This is because CI affects the annual
production per cow. The cost of AI and the work it involves, including heat detection, also
affects the fertility economic value. Insemination data is registered by AI-technicians and
farmers and calvings are registered by farmers (Interbull, 2019b; NAV Nordic Cattle
Genetic Evaluation, 2019b).

There are five fertility traits included in the female fertility breeding value in the NTM: (1)
Heifer IFL, (2) Cow ICF, (3) Cow, IFL, (4) Heifer AIS and (5) Cow AIS. Also considered
in the fertility evaluation is NRR (56 days), CR and heat strength (HST), but HST only in
Sweden (NAV Nordic Cattle Genetic Evaluation, 2019b). A multi-trait animal model is
used to estimate breeding values. Heifer traits are separate traits from cow traits. Different
lactations (lactation 1, 2 and 3) are also considered as separate traits in a multi-trait multi-
lactation analysis. Fertility traits are clustered into three groups for analysis: (1) NRR0,
IFL0, NRR1-3, ICF1-3, IFL1-3, (2) AIS0, HST0, AIS1-3, HST1-3, ICF1-3, (3) CR0, CR1-3.
Different models are used for different fertility traits. Fixed effects included in the models
(depending on the trait) are: herd × first calving year, first insemination year × month ×
country, age at first insemination in heifers × country, calving year × month × country, semen type of first insemination × time-period × country, insemination number. Random effects are animal and in the model for CR, permanent environment. Heterosis is included as a regression in the models (NAV Nordic Cattle Genetic Evaluation, 2019b).

In the fertility index, the estimated breeding values (EBV) are combined by weighting them with their respective economic values (Table 1). IFL₀ and AIS₀ are maiden heifer traits and ICF₁-₃, IFL₁-₃, and AIS₁-₃ are traits in lactations 1, 2 and 3 (NAV Nordic Cattle Genetic Evaluation, 2019b).

<table>
<thead>
<tr>
<th>Breed</th>
<th>Index calculation</th>
</tr>
</thead>
<tbody>
<tr>
<td>HOL</td>
<td>0.73 × IFL₀ + 0.62 × ICF₁-₃ + 2.35 × IFL₁-₃ + 10.17 × AIS₀ + 35.55 × AIS₁-₃</td>
</tr>
<tr>
<td>RDC</td>
<td>0.61 × IFL₀ + 0.56 × ICF₁-₃ + 1.78 × IFL₁-₃ + 10.14 × AIS₀ + 27.24 × AIS₁-₃</td>
</tr>
<tr>
<td>JER</td>
<td>0.93 × IFL₀ + 0.28 × ICF₁-₃ + 1.61 × IFL₁-₃ + 9.27 × AIS₀ + 27.14 × AIS₁-₃</td>
</tr>
</tbody>
</table>

2.7.2 Norway

The main dairy breed in Norway is the Norwegian Red and the breeding organization is Geno. A Total Merit Index (TMI) has been used since 1978 to identify the best Norwegian Red bulls. Fertility has been included in the Norwegian Red breeding program since 1971 and the breed is one of the most fertile dairy cattle breeds in the world according to the breeding organization (Norwegian Red, 2018). All inseminations are reported by AI-technicians and veterinarians. Farmers or advisors report natural services (Interbull, 2019). The Norwegian Red website states that daughter fertility has a weight of 13.87% in the TMI. In the TMI, the daughter fertility index consists of three traits: Heifer AIS (22%), Cow AIS (45%) and ICF (33%). Recently the fertility index was changed when AIS replaced non-return rate (Norwegian Red, 2018).

There are two different models used for predicting GEBVs (genomic EBVs) for fertility traits in Norway. Both of them are multi-trait animal models. The first model is a repeatability model where three traits are run together (different lactations as repeated measurements): 1) AIS, 2) ICF (on a log scale), and 3) kg protein over a 305 lactation. From this model, AIS and ICF are used in the TMI. Fixed effects included in the model
are: age in months at insemination (AIS) / calving (ICF), feeding system, milking system, year × month at calving, herd × n years. In the model of for kg protein 305d, days open period is an additional fixed effect. Random effects are herd × year, additive genetic (animal), permanent environment and residual (Nordbø, 2019, personal communication).

The second model is similar, but it is not a repeatability model because it includes a heifer fertility trait that is not repeated. In this run, only the heifer trait is utilized in the TMI. Four traits are run together: (1) AIS heifer, (2), AIS 1st lactation, (3) ICF 1st lactation (on a log scale), and (4) kg protein 305d, 1st lactation. Fixed effects included in the model are: age in months at insemination (AIS) / calving (ICF), feeding system, milking system, year × month at insemination (AIS) / calving (ICF), herd × n years heifer and for kg protein 305d days open period. Random effects are herd × year heifer, herd × year cow, additive genetic (animal), and residual (Ø. Nordbø, 2019, personal communication).

2.7.3 Germany, Austria and Luxemburg

In Germany, Austria and Luxemburg the company Vereinigte Informationssysteme Tierhaltung w.V. (vit) carries out a joint breeding value evaluation for dairy cattle. Farmers and AI-technicians report inseminations. In the total merit index for all cattle breeds, fertility weighs 10%. Heifer and cow traits are treated as (partly) independent traits. A BLUP multi-trait animal model with repeated observations is used for evaluating daughter fertility. The traits that are used are (1) NRR after 56 days for heifers and cows, (2) IFL for heifers and cows, (3) ICF for cows. The fixed effects used in the model are: herd × year, month of insemination, age at insemination, parity × age at insemination, status of insemination bull, effect of insemination bull × kind-of semen (Interbull, 2019; Vereinigte Informationssysteme Tierhaltung, 2019).

2.7.4 United Kingdom

EGENES provides genetic evaluations for dairy cattle in the UK. A multi-trait animal model BLUP is used and the fertility traits are: (1) NRR at 56 days and (2) CI between 1st and 2nd calving. Also considered in the model are daily milk yield test nearest to 100 days, ICF, AIS and condition score (Interbull, 2019).
2.7.5 United States of America

Council on Dairy Cattle Breeding provides genetic evaluations for dairy cattle in the USA. Fertility traits used are: (1) Heifer conception rate (HCR), percentage of inseminated heifers that become pregnant at each service. (2) ICF, estimated as a linear function of predicted transmitting ability for CCR and DPR. (3) Cow conception rate (CCR), percentage of inseminated cows that become pregnant at each service. (4) Daughter pregnancy rate (DPR), percentage of non-pregnant cows that become pregnant during each 21-day period. A multi-trait, multi-breed animal model BLUP is used to evaluate breeding values (Interbull, 2019).

2.7.6 Canada

Canadian Dairy Network provides genetic evaluations for dairy cattle in Canada. Fertility traits used are (1) NRR at 56 days for heifers and cows, (2) ICF for cows, (3) IFL for cows, (4) ICL/DO for cows. A multi-trait animal model is used with repeated cow records (Interbull, 2019).

2.8 Model Options

Linear models have been widely used in routine genetic evaluations of female fertility traits even though threshold models would perhaps be more appropriate for binary traits e.g. CR and NRR. Threshold models have high computational requirements which makes them hard to use in routine genetic evaluations of large dairy cattle populations. Studies have shown that linear models perform similarly to threshold models but have less computational demand (Andersen-Ranberg et al., 2005b; Liu et al., 2017; Mrode, 2005).
3 Material and Methods

3.1 Data

Data for this study were obtained from the database of the Farmers Association of Iceland. Originally two data files were obtained. The first one contained information about 105,162 animals, including Animal ID, birth herd, production herd, cattle association no., area in Iceland, birth date, culling date, the reason for culling and calving dates 1, 2, 3 and 4. The second file contained information about 411,684 artificial inseminations that took place in the years 2008-2018. This file contained: Animal ID, day of insemination, technician no., AI bull ID, comments and use of SpermVital type semen or not. Only inseminations in the first three lactations and inseminations of maiden heifers were included.

Pedigree data was provided by the Farmers Association of Iceland. The pedigree file was built using a sire-dam structure. The pedigree was traced back 10 generations and pruned for non-informative animals for the evaluation. There were 129,768 individuals in the pedigree file.

The datafiles were combined in a way that each animal had one record line with all relevant information regarding inseminations and calving dates. Calving and insemination dates were used to define fertility traits to be used in the analyses: CI_{12, 23, 34}, AIS_{0, 1, 2, 3}, CR_{0, 1, 2, 3}, IFL_{0, 1, 2, 3}, ICF_{1, 2, 3}, ICL_{1, 2, 3} (Subscript defines lactations 1-3 and 0 is maiden heifers. C as a subscript defines a cow trait where lactations are repeated measurements. In the case of CI, subscript defines an interval between two calvings e.g. CI_{12} means Calving Interval between first and second calving). A further illustration of the traits examined in the study can be seen in Figure 1. Other traits included in data were: Lifespan, number of calvings in data, interval from last insemination to calving (gestation length), age at first insemination (AFI) and age at first calving (AFC).
Date of birth and culling, calving dates and insemination dates were turned into SAS dates to determine intervals between two dates and create the traits AFI, AFC, CI, IFL, ICF and ICL. Lactation numbers were defined by calving dates. Inseminations within each lactation were counted for the AIS$_{0-3}$ traits. CR was defined in a way that if IFL$_{0-3}$ was 0-4 days and the animal calved 260-302 days later CR$_{0-3}$ was 1 (success). If IFL$_{0-3}$ was more than 5 days and the animal calved 260-302 days later CR$_{0-3}$ was 0 (failure). If the animal was inseminated at least once and did not calve CR$_{0-3}$ was 0 (failure).

The data was filtered before analysis, and restrictions were put on records in the data to exclude animals with errors in recording of the inseminations or calvings. While editing data, intervals were kept if within the following limits: AFC 550-1100 days, CI 280-600 days, AFI 270-900 days, ICF 20-230 days, IFL 0-365 days, ICL 20-365 days, gestation length 260-302 days and AIS 1-8. Animals that had specific comments about any insemination, such as “Cow not in estrous”, “Synchronized” or “Cow already pregnant”, were also deleted, as well as animals that had been inseminated with SpermVital semen. Records for later lactations were excluded if information about previous lactations were not available. Animals had to be born in the years 2005 to 2016. Distribution of animals by birth years can be seen in Table 2. Herd-Year classes had to have a minimum of 3 animals. After data editing, 52,951 cows with insemination records remained.
Data on lactation yield and test day yield were provided by the Farmers Association of Iceland. Available information about lactation yield in kg milk and kg protein and test day (TD) yield of kg milk and kg protein closest to day 60 and day 80 of lactations 1, 2 and 3 was affixed to animals in the data and the traits kgMilk, kgProtein, TD60Milk, TD60Protein, TD80Milk, TD80Protein were made. The datafile containing lactation yield was already edited in some ways for preparation of genetic evaluation when it was received. The minimum and maximum values for kg milk per lactation was 800-17,000 kg. The range for TD60 was day 50-69 of the lactation and for TD80 it was day 70-89 of the lactation. The minimum and maximum value of kg milk on a TD was 1kg and 60kg which is similar to editing done for the genetic evaluation.

### 3.2 Statistical Analysis

Five different linear models (1-5 below) were used to estimate the (co)variance components of the fertility traits. In the below models \( \beta_i \) is the vector of fixed effects for the \( i \)th trait, \( a_i \) is the vector of random additive genetic effects for the \( i \)th trait, \( pe_i \) is the vector of permanent environmental effects for the \( i \)th trait (models 3, 4 and 5), \( e_i \) is the vector of random residual effects for the \( i \)th trait. \( X_i, Z_i \) and \( W_i \) were the incidence matrices connecting \( \beta, a \) and \( pe \) to \( y_i \). Fixed effects used in the models were \( \text{herd} \times \text{calving year, age at calving (months)} \) and \( \text{insemination year} \times \text{month} \). For heifer traits \( \text{herd} \times \text{birth year} \) and \( \text{age at first insemination (months)} \) was used. \text{AI technician} was an additional effect in CR models. For CI, kgMilk, kgProtein, and TD traits \( \text{calving month} \) was used instead of \( \text{insemination year} \times \text{month} \). Test day (no. of days milking) was an effect in models analysing TD traits. Lactation length was included as a regression in kgMilk and kgProtein models. The decision on which fixed effects to use was based on literature, the current genetic evaluation, trials of significance of different effects using PROC MIXED in SAS along with trial runs of different models in DMU (Madsen & Jensen, 2013; SAS Institute, 2013). Random effects in the models were the genetic effect of animal \( (a) \), a permanent environmental effect \( (pe) \) and residual effect \( (e) \), with (co)variance structures assumed to be \( a \sim N(0, A \otimes G_a), pe \sim N(0, I \otimes P_a) \) and \( e \sim N (0, I \otimes R_e) \), where \( A \) was the additive

<table>
<thead>
<tr>
<th>Birth Year</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>2122</td>
</tr>
<tr>
<td>2006</td>
<td>4757</td>
</tr>
<tr>
<td>2007</td>
<td>4872</td>
</tr>
<tr>
<td>2008</td>
<td>4948</td>
</tr>
<tr>
<td>2009</td>
<td>5050</td>
</tr>
<tr>
<td>2010</td>
<td>4692</td>
</tr>
<tr>
<td>2011</td>
<td>4610</td>
</tr>
<tr>
<td>2012</td>
<td>4669</td>
</tr>
<tr>
<td>2013</td>
<td>4442</td>
</tr>
<tr>
<td>2014</td>
<td>5379</td>
</tr>
<tr>
<td>2015</td>
<td>4835</td>
</tr>
<tr>
<td>2016</td>
<td>2575</td>
</tr>
</tbody>
</table>
genetic relationship matrix, \( G_a \) was the (co)variance matrix of genetic effects, \( I \) was an identity matrix, \( P_a \) was the (co)variance matrix of permanent environmental effect and \( R_a \) was the residual (co)variance matrix. Inbreeding was accounted for.

Multi-trait models were used to analyse covariances between lactations within the same trait. For traits defined in both heifers and cows, a four-trait model (Model 1) was used (AIS\(_0-3\), CR\(_0-3\), IFL\(_0-3\)). \( y_i \) is the vector of observations (\( i = 0, 1, 2, 3 \) representing heifers (0) and lactations 1, 2 and 3).

\[
\begin{bmatrix}
  y_0 \\
  y_1 \\
  y_2 \\
  y_3
\end{bmatrix} =
\begin{bmatrix}
  X_0 & 0 & 0 & 0 \\
  0 & X_1 & 0 & 0 \\
  0 & 0 & X_2 & 0 \\
  0 & 0 & 0 & X_3
\end{bmatrix}
\begin{bmatrix}
  \beta_0 \\
  \beta_1 \\
  \beta_2 \\
  \beta_3
\end{bmatrix} +
\begin{bmatrix}
  Z_0 & 0 & 0 & 0 \\
  0 & Z_1 & 0 & 0 \\
  0 & 0 & Z_2 & 0 \\
  0 & 0 & 0 & Z_3
\end{bmatrix}
\begin{bmatrix}
  a_0 \\
  a_1 \\
  a_2 \\
  a_3
\end{bmatrix} +
\begin{bmatrix}
  e_0 \\
  e_1 \\
  e_2 \\
  e_3
\end{bmatrix}
\] (Model 1)

A three-trait model (Model 2) was used for traits only defined in cows (ICF\(_1-3\), ICL\(_1-3\), CI\(_1-4\)). \( y_i \) was the vector of observations (\( i = 1, 2, 3 \) representing lactations 1, 2 and 3). A three-trait model was also used to estimate correlations between the three heifer traits (AIS\(_0\), IFL\(_0\), CR\(_0\)). \( y_i \) is the vector of observations (\( i = 1, 2, 3 \) representing fertility traits 1, 2 and 3).

\[
\begin{bmatrix}
  y_1 \\
  y_2 \\
  y_3
\end{bmatrix} =
\begin{bmatrix}
  X_1 & 0 & 0 \\
  0 & X_2 & 0 \\
  0 & 0 & X_3
\end{bmatrix}
\begin{bmatrix}
  \beta_1 \\
  \beta_2 \\
  \beta_3
\end{bmatrix} +
\begin{bmatrix}
  Z_1 & 0 & 0 \\
  0 & Z_2 & 0 \\
  0 & 0 & Z_3
\end{bmatrix}
\begin{bmatrix}
  a_1 \\
  a_2 \\
  a_3
\end{bmatrix} +
\begin{bmatrix}
  e_1 \\
  e_2 \\
  e_3
\end{bmatrix}
\] (Model 2)

The cow traits were further analysed using a single-trait model (Model 3) where multiple lactations were repeated measurements (heifer records not included).

\[
y = X\beta + Za + Wpe + e
\] (Model 3)

To estimate correlations between a pair of cow traits (AIS\(_c\), CR\(_c\), IFL\(_c\), ICF\(_c\), ICL\(_c\), CI\(_c\)) a two-trait model (Model 4) was used. \( y_i \) is the vector of observations (\( i = 1, 2 \) representing fertility traits 1 and 2).

\[
\begin{bmatrix}
  y_1 \\
  y_2
\end{bmatrix} =
\begin{bmatrix}
  X_1 & 0 \\
  X_2 & Z_2
\end{bmatrix}
\begin{bmatrix}
  \beta_1 \\
  \beta_2
\end{bmatrix} +
\begin{bmatrix}
  Z_1 & 0 \\
  0 & Z_2
\end{bmatrix}
\begin{bmatrix}
  a_1 \\
  a_2
\end{bmatrix} +
\begin{bmatrix}
  W_1 & 0 \\
  0 & W_2
\end{bmatrix}
\begin{bmatrix}
  pe_1 \\
  pe_2
\end{bmatrix} +
\begin{bmatrix}
  e_1 \\
  e_2
\end{bmatrix}
\] (Model 4)

To estimate correlations between a fertility trait and two yield traits (milk and protein yield) a three-trait model (Model 5) was used. Multiple lactations were repeated measurements. \( y_i \) was the vector of observations (\( i = 1 \) representing a fertility trait and 2, 3
the yield traits). (In addition, lactation length in days was included as a regression in kgMilk and kgProtein models.)

\[
\begin{pmatrix}
y_1 \\
y_2 \\
y_3
\end{pmatrix} = 
\begin{pmatrix}
X_1 & 0 & 0 \\
0 & X_2 & 0 \\
0 & 0 & X_3
\end{pmatrix}
\begin{pmatrix}
\beta_1 \\
\beta_2 \\
\beta_3
\end{pmatrix} + 
\begin{pmatrix}
Z_1 & 0 & 0 \\
0 & Z_2 & 0 \\
0 & 0 & Z_3
\end{pmatrix}
\begin{pmatrix}
\alpha_1 \\
\alpha_2 \\
\alpha_3
\end{pmatrix} + 
\begin{pmatrix}
W_1 & 0 & 0 \\
0 & W_2 & 0 \\
0 & 0 & W_3
\end{pmatrix}
\begin{pmatrix}
pe_1 \\
p_2 \\
pe_3
\end{pmatrix} + 
\begin{pmatrix}
e_1 \\
e_2 \\
e_3
\end{pmatrix} \tag{Model 5}
\]

The statistical software SAS 9.4 (SAS Institute, 2013) was used in basic data handling. (Co)variance components were estimated using the AI-algorithm in the DMU-package (Madsen & Jensen, 2013). Standard errors of heritability values from models 3, 4 and 5 were approximated from asymptotic standard errors of (co)variance components in the output from DMU (Madsen & Jensen, 2013) using Taylor series expansion as was described in Albertsdóttir et al. (2007).

Breeding values were estimated using the DMU5 software with the same data as was used for previous analysis in the study. EBVs were used to investigate genetic trends. The same models were used for estimation of breeding values as for the estimation of variance components within each trait (Models 1 and 2). Genetic trends of the fertility traits were further analysed using single-trait models (Model 3) where lactations were treated as repeated measurements.
4 Results

The average age of first insemination for heifers was 527 ± 99.8 days. The average age of first calving for cows was 832 ± 104.6 days. In the data, 51% of the cows had recorded insemination as a maiden heifer and 93% of the cows had a recorded first calving. Figure 4 in Appendix II shows how many recorded calvings there were for the cows in the data. The proportion of animals that had recorded heifer insemination and recorded first calving was 87%. The proportion of cows that were inseminated in lactation one, two and three and had a recorded calving two, three and four were 86%, 87% and 85% respectively.

Phenotypic averages for heifers and cows in the first three lactations for the six fertility traits analysed can be seen in Table 3.

Average phenotypic values for AIS and CR were more favourable for heifers (1.57 and 0.62) than for cows (1.72-1.78 for AIS and 0.50-0.52 for CR, respectively). CR was lowest in the third lactation (0.50). Average phenotypic values for AIS, IFL, ICF, ICL and CI were more favourable in the second lactation than in the first and the third lactation.

Variance components and heritability estimates for the fertility traits are shown in Table 4 and Table 5. Estimated heritabilities using multi-trait models (Models 1 and 2) were low for all fertility traits, ranging from 0.010 (IFL_0) to 0.081 (ICF_2). Standard errors for the

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Mean±SD</th>
<th>Min-Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR_0</td>
<td>27236</td>
<td>0.62±0.48</td>
<td>0-1</td>
</tr>
<tr>
<td>CR_1</td>
<td>42871</td>
<td>0.51±0.50</td>
<td>0-1</td>
</tr>
<tr>
<td>CR_2</td>
<td>26044</td>
<td>0.52±0.50</td>
<td>0-1</td>
</tr>
<tr>
<td>CR_3</td>
<td>14860</td>
<td>0.50±0.50</td>
<td>0-1</td>
</tr>
<tr>
<td>AIS_0</td>
<td>27236</td>
<td>1.57±0.99</td>
<td>1-8</td>
</tr>
<tr>
<td>AIS_1</td>
<td>42871</td>
<td>1.78±1.15</td>
<td>1-8</td>
</tr>
<tr>
<td>AIS_2</td>
<td>26044</td>
<td>1.72±1.11</td>
<td>1-8</td>
</tr>
<tr>
<td>AIS_3</td>
<td>14860</td>
<td>1.75±1.14</td>
<td>1-8</td>
</tr>
<tr>
<td>IFL_0</td>
<td>27236</td>
<td>25.8±58.5</td>
<td>0-365</td>
</tr>
<tr>
<td>IFL_1</td>
<td>42871</td>
<td>25.8±43.8</td>
<td>0-308</td>
</tr>
<tr>
<td>IFL_2</td>
<td>26044</td>
<td>24.0±42.1</td>
<td>0-325</td>
</tr>
<tr>
<td>IFL_3</td>
<td>14860</td>
<td>24.9±42.5</td>
<td>0-303</td>
</tr>
<tr>
<td>ICF_1</td>
<td>42871</td>
<td>82.4±33.8</td>
<td>20-230</td>
</tr>
<tr>
<td>ICF_2</td>
<td>26044</td>
<td>79.6±31.9</td>
<td>20-230</td>
</tr>
<tr>
<td>ICF_3</td>
<td>14860</td>
<td>80.4±32.0</td>
<td>20-230</td>
</tr>
<tr>
<td>ICL_1</td>
<td>42871</td>
<td>108.1±53.3</td>
<td>20-365</td>
</tr>
<tr>
<td>ICL_2</td>
<td>26044</td>
<td>103.6±50.5</td>
<td>20-364</td>
</tr>
<tr>
<td>ICL_3</td>
<td>14860</td>
<td>105.3±50.9</td>
<td>20-361</td>
</tr>
<tr>
<td>CI_12</td>
<td>36729</td>
<td>389.8±50.1</td>
<td>286-600</td>
</tr>
<tr>
<td>CI_23</td>
<td>22632</td>
<td>384.9±46.8</td>
<td>287-599</td>
</tr>
<tr>
<td>CI_34</td>
<td>12570</td>
<td>386.8±47.4</td>
<td>288-600</td>
</tr>
</tbody>
</table>

aCR conception rate at first insemination, AIS number of inseminations per service period, IFL interval first to last insemination, ICF interval calving to first insemination, ICL interval calving to last insemination, CI calving interval. 0 = heifers, 1, 2 and 3 = lactations.
heritability estimates ranged from 0.004 to 0.012 using multi-trait models. For the traits ICF, ICL and CI heritability estimates were highest in the second lactation. These three traits also had higher heritabilities than the other three traits (CR, AIS and IFL). This was also the case using single-trait models where lactations were treated as repeated measurements (Model 3). When using Model 3, heritabilities ranged from 0.017 (CRc) to 0.060 (ICFc). Standard errors for the heritability estimates ranged from 0.003 to 0.007 using single-trait models.

<table>
<thead>
<tr>
<th>Traitb</th>
<th>σ²σ²</th>
<th>σ²e</th>
<th>h² (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR₀</td>
<td>3.44 E-03</td>
<td>0.210</td>
<td><strong>0.016</strong> (0.005)</td>
</tr>
<tr>
<td>CR₁</td>
<td>4.81 E-03</td>
<td>0.231</td>
<td><strong>0.020</strong> (0.005)</td>
</tr>
<tr>
<td>CR₂</td>
<td>4.91 E-03</td>
<td>0.230</td>
<td><strong>0.021</strong> (0.006)</td>
</tr>
<tr>
<td>CR₃</td>
<td>6.49 E-03</td>
<td>0.234</td>
<td><strong>0.027</strong> (0.010)</td>
</tr>
<tr>
<td>AIS₀</td>
<td>0.012</td>
<td>0.864</td>
<td><strong>0.014</strong> (0.005)</td>
</tr>
<tr>
<td>AIS₁</td>
<td>0.024</td>
<td>1.177</td>
<td><strong>0.020</strong> (0.004)</td>
</tr>
<tr>
<td>AIS₂</td>
<td>0.027</td>
<td>1.111</td>
<td><strong>0.024</strong> (0.007)</td>
</tr>
<tr>
<td>AIS₃</td>
<td>0.023</td>
<td>1.202</td>
<td><strong>0.019</strong> (0.008)</td>
</tr>
<tr>
<td>IFL₀</td>
<td>30.8</td>
<td>3101.3</td>
<td><strong>0.010</strong> (0.005)</td>
</tr>
<tr>
<td>IFL₁</td>
<td>43.5</td>
<td>1731.8</td>
<td><strong>0.025</strong> (0.005)</td>
</tr>
<tr>
<td>IFL₂</td>
<td>28.2</td>
<td>1632.1</td>
<td><strong>0.017</strong> (0.006)</td>
</tr>
<tr>
<td>IFL₃</td>
<td>43.2</td>
<td>1700.0</td>
<td><strong>0.025</strong> (0.010)</td>
</tr>
<tr>
<td>ICF₁</td>
<td>37.7</td>
<td>652.0</td>
<td><strong>0.055</strong> (0.008)</td>
</tr>
<tr>
<td>ICF₂</td>
<td>57.6</td>
<td>653.7</td>
<td><strong>0.081</strong> (0.012)</td>
</tr>
<tr>
<td>ICF₃</td>
<td>32.2</td>
<td>705.7</td>
<td><strong>0.044</strong> (0.011)</td>
</tr>
<tr>
<td>ICL₁</td>
<td>78.8</td>
<td>2225.3</td>
<td><strong>0.034</strong> (0.006)</td>
</tr>
<tr>
<td>ICL₂</td>
<td>93.7</td>
<td>2118.0</td>
<td><strong>0.042</strong> (0.009)</td>
</tr>
<tr>
<td>ICL₃</td>
<td>60.7</td>
<td>2236.4</td>
<td><strong>0.026</strong> (0.010)</td>
</tr>
<tr>
<td>CI₁₂</td>
<td>77.3</td>
<td>2038.2</td>
<td><strong>0.037</strong> (0.007)</td>
</tr>
<tr>
<td>CI₁₃</td>
<td>80.1</td>
<td>1870.0</td>
<td><strong>0.041</strong> (0.009)</td>
</tr>
<tr>
<td>CI₁₄</td>
<td>37.4</td>
<td>2012.5</td>
<td><strong>0.018</strong> (0.010)</td>
</tr>
</tbody>
</table>

*σ²σ²/ σ²e = additive genetic variance / residual variance using multi-trait models (Model 1 and 2), h² = estimated heritability.

bCR conception rate at first insemination, AIS number of inseminations per service period, IFL interval first to last insemination, ICF interval calving to first insemination, ICL interval calving to last insemination, CI calving interval. 0 = heifers, 1, 2 and 3 = lactations.
Phenotypic averages for the yield traits used in the study are presented in Table 17 in Appendix II. Variance components and heritabilities estimated for the yield traits using a single-trait model (Model 3) are shown in Table 18 in Appendix II. Heritability estimates were highest for kgMilk<sub>c</sub> and kgProtein<sub>c</sub>, 0.245 and 0.218 respectively. Heritability for TD traits ranged from 0.151 to 0.187. Standard errors for yield trait heritability estimates ranged from 0.011 to 0.014.

Genetic correlation between lactations within traits using multi-trait models (Models 1 and 2) can be seen in Table 6. Genetic correlations between performance in heifers and cows were weak to moderate for IFL (0.23-0.44), moderate for CR (0.40-0.60) and strong for AIS (0.64-0.81). Genetic correlations between first and second lactation were strong to very strong (0.82-0.96) in all cases except for CR where it was 0.36. Genetic correlations between first and third lactation were strong to very strong for AIS, ICF and CI (0.81-0.95) but moderate for CR, IFL and ICL (0.37-0.60). Genetic correlations between second and third lactation were strong to very strong in all traits (0.79-1.00). Phenotypic correlations were very weak between parities within traits.

**Table 5 - Variance components<sup>a</sup> for fertility traits using single-trait models.**

<table>
<thead>
<tr>
<th>Trait&lt;sup&gt;b&lt;/sup&gt;</th>
<th>σ&lt;sup&gt;2&lt;/sup&gt;&lt;sub&gt;a&lt;/sub&gt;</th>
<th>σ&lt;sup&gt;2&lt;/sup&gt;&lt;sub&gt;pe&lt;/sub&gt;</th>
<th>σ&lt;sup&gt;2&lt;/sup&gt;&lt;sub&gt;e&lt;/sub&gt;</th>
<th>h&lt;sup&gt;2&lt;/sup&gt; (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR&lt;sub&gt;c&lt;/sub&gt;</td>
<td>4.13E-03</td>
<td>4.90E-03</td>
<td>0.228</td>
<td>0.017 (0.003)</td>
</tr>
<tr>
<td>AIS&lt;sub&gt;c&lt;/sub&gt;</td>
<td>0.024</td>
<td>0.064</td>
<td>1.103</td>
<td>0.020 (0.004)</td>
</tr>
<tr>
<td>IFL&lt;sub&gt;c&lt;/sub&gt;</td>
<td>35.9</td>
<td>66.6</td>
<td>1647.8</td>
<td>0.021 (0.004)</td>
</tr>
<tr>
<td>ICF&lt;sub&gt;c&lt;/sub&gt;</td>
<td>43.5</td>
<td>26.7</td>
<td>631.8</td>
<td>0.060 (0.007)</td>
</tr>
<tr>
<td>ICL&lt;sub&gt;c&lt;/sub&gt;</td>
<td>78.5</td>
<td>113.8</td>
<td>2116.7</td>
<td>0.034 (0.005)</td>
</tr>
<tr>
<td>CI&lt;sub&gt;c&lt;/sub&gt;</td>
<td>77.8</td>
<td>105.6</td>
<td>1912.5</td>
<td>0.037 (0.005)</td>
</tr>
</tbody>
</table>

<sup>a</sup>σ<sup>2</sup><sub>a</sub>/σ<sup>2</sup><sub>pe</sub>/σ<sup>2</sup><sub>e</sub> = additive genetic variance / permanent environmental variance / residual variance of a cow trait using a single-trait model where lactations were repeated measurements (Model 3). h<sup>2</sup> = estimated heritability of a cow traits using a single-trait model where lactations were repeated measurements (Model 3).

<sup>b</sup>CR conception rate at first insemination, AIS number of inseminations per service period, IFL interval first to last insemination, ICF interval calving to first insemination, ICL interval calving to last insemination, CI calving interval. 0 = heifers, 1, 2 and 3 = lactations.
Table 6 – Genetic correlations between fertility traits in different parities using a multi-trait model (Model 1 and 2).

<table>
<thead>
<tr>
<th>Trait</th>
<th>( r_{a0a1} )</th>
<th>( r_{a0a2} )</th>
<th>( r_{a0a3} )</th>
<th>( r_{a1a2} )</th>
<th>( r_{a1a3} )</th>
<th>( r_{a2a3} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR</td>
<td>0.60</td>
<td>0.44</td>
<td>0.40</td>
<td>0.36</td>
<td>0.37</td>
<td>0.91</td>
</tr>
<tr>
<td>AIS</td>
<td>0.64</td>
<td>0.81</td>
<td>0.74</td>
<td>0.82</td>
<td>0.86</td>
<td>0.99</td>
</tr>
<tr>
<td>IFL</td>
<td>0.35</td>
<td>0.44</td>
<td>0.23</td>
<td>0.82</td>
<td>0.52</td>
<td>0.79</td>
</tr>
<tr>
<td>ICF</td>
<td></td>
<td></td>
<td></td>
<td>0.96</td>
<td>0.95</td>
<td>0.88</td>
</tr>
<tr>
<td>ICL</td>
<td></td>
<td></td>
<td></td>
<td>0.85</td>
<td>0.60</td>
<td>0.93</td>
</tr>
<tr>
<td>CI</td>
<td></td>
<td></td>
<td></td>
<td>0.86</td>
<td>0.81</td>
<td>~1.00</td>
</tr>
</tbody>
</table>

\( r_{a0a1} \), \( r_{a0a2} \), \( r_{a0a3} \), \( r_{a1a2} \), \( r_{a1a3} \), and \( r_{a2a3} \) represent genetic correlations within a trait between parities 0 and 1, 0 and 2, 0 and 3, 1 and 2, 1 and 3, and 2 and 3, respectively.

<table>
<thead>
<tr>
<th>Trait</th>
<th>CR ( _0 )</th>
<th>AIS ( _0 )</th>
<th>IFL ( _0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR ( _0 )</td>
<td>-0.98 (0.06)</td>
<td>-0.90 (0.11)</td>
<td></td>
</tr>
<tr>
<td>AIS ( _0 )</td>
<td>-0.67</td>
<td>0.87 (0.10)</td>
<td></td>
</tr>
<tr>
<td>IFL ( _0 )</td>
<td>-0.56</td>
<td>0.73</td>
<td></td>
</tr>
</tbody>
</table>

Genetic and phenotypic correlations between the three heifer traits (Model 2) are shown in Table 7. Genetic correlations were strong between all traits, negative between CR\( _0 \)-AIS\( _0 \) and CR\( _0 \)-IFL\( _0 \) and positive between AIS\( _0 \) and IFL\( _0 \). Phenotypic correlations were moderate or strong between all traits.

Table 7 - Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between heifer traits using a three-trait model (Model 2).

<table>
<thead>
<tr>
<th>Trait</th>
<th>CR ( _0 )</th>
<th>AIS ( _0 )</th>
<th>IFL ( _0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR ( _0 )</td>
<td>-0.98 (0.06)</td>
<td>-0.90 (0.11)</td>
<td></td>
</tr>
<tr>
<td>AIS ( _0 )</td>
<td>-0.67</td>
<td>0.87 (0.10)</td>
<td></td>
</tr>
<tr>
<td>IFL ( _0 )</td>
<td>-0.56</td>
<td>0.73</td>
<td></td>
</tr>
</tbody>
</table>

\( CR \) conception rate at first insemination, \( AIS \) number of inseminations per service period, \( IFL \) interval first to last insemination, \( ICL \) interval calving to first insemination, \( ICF \) interval calving to last insemination, \( CI \) calving interval. 0 = heifers, 1, 2 and 3 = lactations.

Phenotypic correlations ranged from 0.01 to 0.11.

SE ranged from 0.13 to 0.28.
Genetic and phenotypic correlations between cow traits when lactations were treated as repeated measurements in a two-trait model (Model 4) are presented in Table 8. There were strong negative genetic correlations between CRc-AISc as well as CRc-IFLc, and moderate negative genetic correlations between CRc-ICLc and CRc-CIc. There was a very strong positive genetic correlation between IFLc and AISc and also between ICLc and CIc. There were weak genetic correlations between ICFc and the traits CRc, AISc and IFLc.

<table>
<thead>
<tr>
<th>Traita</th>
<th>CRc</th>
<th>AISc</th>
<th>IFLc</th>
<th>ICFc</th>
<th>ICLc</th>
<th>CIc</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRc</td>
<td>0.81</td>
<td>-0.80</td>
<td>0.01</td>
<td>-0.57</td>
<td>-0.63</td>
<td></td>
</tr>
<tr>
<td>AISc</td>
<td>-0.62</td>
<td>0.94</td>
<td>0.17</td>
<td>0.51</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>IFLc</td>
<td>-0.58</td>
<td>0.81</td>
<td>0.09</td>
<td>0.70</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>ICFc</td>
<td>0.04</td>
<td>-0.06</td>
<td>0.04</td>
<td>0.77</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>ICLc</td>
<td>-0.49</td>
<td>0.67</td>
<td>0.83</td>
<td>0.50</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td>CIc</td>
<td>-0.60</td>
<td>0.71</td>
<td>0.90</td>
<td>0.57</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Traita</th>
<th>CRc</th>
<th>AISc</th>
<th>IFLc</th>
<th>ICFc</th>
<th>ICLc</th>
<th>CIc</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRc</td>
<td>0.81</td>
<td>-0.80</td>
<td>0.01</td>
<td>-0.57</td>
<td>-0.63</td>
<td></td>
</tr>
<tr>
<td>AISc</td>
<td>-0.62</td>
<td>0.94</td>
<td>0.17</td>
<td>0.51</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>IFLc</td>
<td>-0.58</td>
<td>0.81</td>
<td>0.09</td>
<td>0.70</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>ICFc</td>
<td>0.04</td>
<td>-0.06</td>
<td>0.04</td>
<td>0.77</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>ICLc</td>
<td>-0.49</td>
<td>0.67</td>
<td>0.83</td>
<td>0.50</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td>CIc</td>
<td>-0.60</td>
<td>0.71</td>
<td>0.90</td>
<td>0.57</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>

*CR* conception rate at first insemination, *AIS* number of inseminations per service period, *IFL* interval from first to last insemination, *ICF* interval from calving to first insemination, *ICL* interval from calving to last insemination, *CI* calving interval.

SE for genetic correlations ranged from 0.00 to 0.11.

Genetic correlations between the six fertility traits and 1) kgMilkc and kgProtein, 2) TD60Milkc and TD60Protein, and 3) TD80Milkc and TD80Protein using a three-trait model where lactations were treated as repeated measurements (Model 5) are shown in Table 9. Genetic correlations with production (kgMilkc and kgProtein) were moderate for AISc, IFLc, ICLc and CIc (0.41-0.53) and weak for CRc (-0.19 to -0.22) and ICFc (0.16-0.22). Genetic correlations with TD60Milk/Protein were weak for AISc, IFLc, ICLc and CIc and very weak for CRc and ICFc. Genetic correlations between TD80Milk/Protein were very weak for CRc and ICFc and weak/moderate for AISc, IFLc, ICLc and CIc (0.33-0.43).
Table 9 - Genetic correlations between fertility traits and yield traits using a three-trait model (Model 5). *(Phenotypic correlations in parentheses).*

<table>
<thead>
<tr>
<th>Trait</th>
<th>kgMilk</th>
<th>kgProtein</th>
<th>TD60Milk</th>
<th>TD60Protein</th>
<th>TD80Milk</th>
<th>TD80Protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR</td>
<td>-0.22</td>
<td>-0.19</td>
<td>0.08</td>
<td>0.04</td>
<td>-0.10</td>
<td>-0.09</td>
</tr>
<tr>
<td>AIS</td>
<td>0.43</td>
<td>0.41</td>
<td>0.20</td>
<td>0.22</td>
<td>0.35</td>
<td>0.36</td>
</tr>
<tr>
<td>IFL</td>
<td>0.45</td>
<td>0.44</td>
<td>0.24</td>
<td>0.26</td>
<td>0.36</td>
<td>0.38</td>
</tr>
<tr>
<td>ICF</td>
<td>0.22</td>
<td>0.16</td>
<td>0.09</td>
<td>-0.00</td>
<td>0.18</td>
<td>0.08</td>
</tr>
<tr>
<td>ICL</td>
<td>0.48</td>
<td>0.43</td>
<td>0.25</td>
<td>0.21</td>
<td>0.39</td>
<td>0.34</td>
</tr>
<tr>
<td>CI</td>
<td>0.53</td>
<td>0.45</td>
<td>0.29</td>
<td>0.21</td>
<td>0.43</td>
<td>0.33</td>
</tr>
</tbody>
</table>

*CR* conception rate at first insemination, *AIS* number of inseminations per service period, *IFL* interval first to last insemination, *ICF* interval calving to first insemination, *ICL* interval calving to last insemination, *CI* calving interval, *kgMilk* kg of milk over a lactation, *kgProtein* kg of protein over a lactation, *TD60Milk*/*TD60Protein*, *TD80Milk*/*TD80Protein* kg of milk/protein on a test day close to day 60/80 of the lactation (range of days are day 50-69 of the lactation for TD60 and day 70-89 of the lactation for TD80).

SE ranged from 0.05 to 0.09.

Estimated genetic trends for all six fertility traits shown in Figure 2. The traits CR₀-₃ showed no clear trends. The genetic trends for AIS₀-₃ were quite stable and unfavourable. For IFL₀-₃ the genetic trends were slightly positive and unfavourable. The genetic trends for ICF₁-₃ were clearly negative and favourable. For the ICL₁-₃ the genetic trends were slightly negative and favourable. The genetic trends for CI₁-₄ were mostly positive and unfavourable but there were some differences between years, e.g. a favourable drop for animals born in 2010.
Figure 2 – Genetic trends (mean EBVs per birth year from DMU5) for animals in the analysed dataset with own observations for the six fertility traits estimated with multi-trait models within each trait (Models 1 and 2): a) CR conception rate at first insemination, b) AIS number of inseminations per service period, c) IFL interval first to last insemination, d) ICF interval calving to first insemination, e) ICL interval calving to last insemination, f) CI calving interval. 0 = heifers, 1, 2 and 3 = lactations. The scale of the y-axis is the same for a) CR and b) AIS and the same for c) IFL, d) ICF, e) ICL and f) CI. The average values in the beginning and end of each trend generally include fewer EBVs.
Estimated genetic trends for all six fertility traits where lactations were repeated measurements are shown in Figure 3. CI, IFL and AIS showed positive unfavourable trends. ICF, as well as ICL, showed negative favourable trends. The genetic trend for CR was slightly negative and unfavourable in the first year but the trend was more unclear during the last few years.

**Figure 3** - Genetic trends (mean EBVs per birth year from DMU5) for animals in the analysed dataset using a six-trait model where lactations are repeated measurements but zero correlations between traits were used in the estimation. a) CR conception rate at first insemination, b) AIS number of inseminations per service period, c) IFL interval first to last insemination, d) ICF interval calving to first insemination, e) ICL interval calving to last insemination, f) CI calving interval. The left y-axis is for IFL, ICF, ICL and CI and the right y-axis is for CR and AIS.

Spearman rank correlations between EBVs in a few traits for both cows with own observations and bulls with more than 10 daughters in the analysed dataset can be seen in Table 10. There were moderate correlations between EBVs for ICF-CI and IFL-CI in first and second lactation. Correlations between ICF<sub>c</sub>-ICF<sub>1</sub> and ICF<sub>c</sub>-ICF<sub>2</sub> and between IFL<sub>c</sub>-IFL<sub>1</sub> and IFL<sub>c</sub>-IFL<sub>2</sub> EBVs were in all cases very strong. The correlation between EBVs for CR<sub>0</sub> and ICF<sub>1</sub> was very weak; between CR<sub>0</sub> and IFL<sub>1</sub> moderate and negative and between CR<sub>0</sub> and CI<sub>12</sub> it was weak and negative.
Table 10 – Spearman rank correlations between EBVs from DMU5 for cows in data with own observations and bulls in pedigree file with 10 or more daughters in the data file of analysed cows.

<table>
<thead>
<tr>
<th>Correlated EBVs</th>
<th>Cows in analysed data (N=52,951)</th>
<th>Bulls with 10+ daughters in analysed data (N=212)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ICF₁ – CI₁₂</td>
<td>0.424</td>
<td>0.494</td>
</tr>
<tr>
<td>ICF₂ – CI₂₃</td>
<td>0.450</td>
<td>0.527</td>
</tr>
<tr>
<td>IFL₁ – CI₁₂</td>
<td>0.681</td>
<td>0.654</td>
</tr>
<tr>
<td>IFL₂ – CI₂₃</td>
<td>0.645</td>
<td>0.617</td>
</tr>
<tr>
<td>ICFᵦ – ICF₁</td>
<td>0.961</td>
<td>0.963</td>
</tr>
<tr>
<td>ICFᵦ – ICF₂</td>
<td>0.942</td>
<td>0.944</td>
</tr>
<tr>
<td>IFLᵦ – IFL₁</td>
<td>0.921</td>
<td>0.910</td>
</tr>
<tr>
<td>IFLᵦ – IFL₂</td>
<td>0.930</td>
<td>0.937</td>
</tr>
<tr>
<td>CR₀ – ICF₁</td>
<td>0.042</td>
<td>-0.002&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>CR₀ – IFL₁</td>
<td>-0.379</td>
<td>-0.386</td>
</tr>
<tr>
<td>CR₀ – CI₁₂</td>
<td>-0.181</td>
<td>-0.188&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>NS</sup> Not significant, >0.05.

CR conception rate at first insemination, IFL interval first to last insemination, ICF interval calving to first insemination, CI calving interval.

Subscript <sub>c</sub> represents a trait where EBVs were estimated with a model where lactations were repeated observations (Model 3). Subscript 0, 1, 2 represent lactation traits that where EBVs were estimated in a multi-trait model as has been previously mentioned and described (Model 1 or 2).
5 Discussion

In this study, I have estimated (co)variance components for six female fertility traits in Icelandic dairy cattle. Relationships between heifers and cows, relationships between lactations within the same trait, along with relationships between different fertility traits were investigated. In addition, relationships between fertility traits and yield traits were analysed. Breeding values and genetic trends for animals in the analysed data were estimated for the six fertility traits. Spearman rank correlations between EBVs for a few traits were analysed.

Below in this discussion, results from the current study are compared to other fertility studies. Because many factors can differ significantly between studies (e.g. trait definition, data editing, management practices) comparisons between e.g. phenotypic values can only be suggestive (Muuttoranta et al., 2019).

5.1 The Fertility Traits on a Phenotypic Level

The average age at first calving in the study was in agreement with the average age at first calving in the record keeping for the Icelandic dairy cattle in 2019 (Ráðgjafamiðstöð landbúnaðarins, 2019). Studies have shown that cows have the greatest economic return when age at first calving is around 2 years (Pirlo et al. 2000; Þórarinsdóttir, 2017). If this is to be achieved, then age at first insemination needs to be reduced to 14-15 months. In this study, the average age at first insemination was much higher (17.5 months), and there is considerable room for improvement in the insemination management by Icelandic dairy farmers.

In the present study, phenotypic values for CR and AIS were more favourable for heifers than for cows, which might suggest heifer fertility on a phenotypic level was better than the fertility of lactating cows in the terms that they needed on average fewer inseminations to conceive. Fewer insemination for heifers could also be management related as farmers choose to use natural service bulls after trying for one insemination of heifers. In the current study however, a limit was set on gestation length so heifers who had subsequent calving should have conceived after insemination, not a natural service. The average CR0 was slightly lower and average CR1-3 were somewhat higher in the current study than in Scandinavian Holstein and Scandinavian RDC (Muuttoranta et al., 2019).
cows average AIS_{1-2} were similar but average AIS_{0} was lower than in the current study (Eriksson et al., 2017).

Even though AIS and IFL should represent the same period, the average phenotypic values of IFL were more favourable for second and third lactation than for heifers and first lactation cows. This difference cannot be readily explained and might come down to data editing, the definition of the traits or farm management related factors (e.g. missed estrous detection of heifers for one cycle). Average phenotypic IFL_{1-3} values in this study were considerably lower (favourable) than in Scandinavian Holstein and RDC (40.7-53.3 days) (Muuttoranta et al., 2019).

In Muuttoranta et al. (2019), average ICF_{1-3} in Scandinavian Holstein were higher (unfavourable) than in the current study but in Scandinavian RDC it was more similar to this study. In Andersen-Ranberg et al. (2005a) the average ICF for first lactation NRF was similar to the current study as well. These similarities suggest the fertility of Nordic cows and the insemination policy in the Nordic countries are in some ways similar to in Iceland.

5.2 Heritability Estimates

Heritability estimates were all low, as was expected, using both multi-trait models and single-trait models. The lowest estimates were found for the three heifer traits. Numerous heritability estimates for these traits from other studies that are often referenced, are given in Tables 11-16 in Appendix I.

Heritabilities of CR_{0-3} were similar to estimates given in other studies (Muuttoranta et al., 2019; de Haer et al., 2013; Tiezzy et al., 2012). In a study by Liu et al. (2017) CR_{1-3} heritabilities were a little lower than in this study. Heritability estimates for AIS_{0-3} and IFL_{0-3} were in a similar range, which could be expected as those traits should represent the same period. Heritabilities of those traits were in general lower in the current study than estimates in other studies (e.g. Eriksson et al., 2017; Liu et al., 2017; Muuttoranta et al., 2019; Tiezzy et al., 2012). This may at least partly be due to differences in environmental factors between countries once the insemination period has started (e.g. management related factors). However, heritabilities of AIS_{0} and IFL_{0} in this study were similar to estimates in studies by Liu et al. (2017) and Muuttoranta et al. (2019).
Out of the six fertility traits analysed in this study, ICF$_{1-3}$ had the highest heritability estimates using a multi-trait model, which is consistent with other studies (de Haer et al., 2013; Liu et al., 2017; Muuttoranta et al., 2019; Tiezzy et al., 2012). ICL is a combination of the traits ICF and IFL. Heritability estimates of ICL$_{1-3}$ were lower than for ICF$_{1-3}$ and higher than for IFL$_{1-3}$ using multi-trait models. Results were in a similar range as estimates given by Roxström et al. (2001) and Liu et al. (2017).

Heritabilities of CI$_{12}$ and CI$_{23}$ were similar to ICL$_1$ and ICL$_2$, which is reasonable since CI is ICL plus gestation length. In the current genetic evaluation for Icelandic dairy cattle, it is assumed that heritabilities of CI$_{12}$, CI$_{23}$ and CI$_{34}$ are 0.04, 0.05 and 0.06, respectively (Sigurðsson, 2007). Heritability of CI$_{12}$ and CI$_{23}$ in the current study were comparable but the estimate of CI$_{34}$ was much lower (0.018). In this study, only one quarter of the analysed cows had own observations for CI$_{34}$. In de Haer et al. (2013) heritability estimates for CI$_{1-4}$ were higher than in the current study, but in Montaldo et al. (2010) CI$_{1-4}$ heritabilities were lower.

When heritabilities were estimated using single-trait models the results were in most cases comparable to other studies with similar estimates (e.g. González-Recio & Alenda, 2005; Liu et al., 2017; Pritchard et al., 2013). The exception was the heritability of IFL$_c$ which was lower in the current study than estimates in other studies, similar to what was seen with the multi-trait model comparisons (González-Recio & Alenda, 2005; Gredler & Schnyder, 2013; Liu et al., 2017).

The most recent study about fertility in Icelandic cattle was made by Ragnarsdóttir (2011). In her study heritabilities were estimated for AIS, ICF, ICL and CI, but those estimates were not directly comparable to the current study. The previous study was much less extensive than the current one, included fewer animals over a shorter time period. In addition, the data editing in the Ragnarsdóttir (2011) study was in some cases not comparable to that in the current study. Comparison of results between these studies should therefore be made with caution.

All yield traits had higher heritability estimates than the fertility traits and heritabilities were higher for kgMilk$_c$ and kgProtein$_c$ than for test day traits. Other fertility studies where
production traits were also analysed showed higher heritability estimates for yield traits than in the current study. In studies by Eriksson et al. (2017) and Sun et al. (2010) heritabilities for either 305-day milk yield and 305-day protein yield ranged from 0.33 to 0.35. In Sewalem et al. (2010) the heritability estimate of test day milk yield closest to day 90 was 0.27. In a recent study by Eiriksson et al. (2019b) heritability estimates for lactation yield in Icelandic cows using a test-day random regression model ranged from 0.33 to 0.43 for milk and protein yield. This was considerably higher than estimates in the current study, but the number of analysed animals and observations were not comparable between the studies and reported heritabilities of yield traits in this study were furthermore analysed using single-trait repeatability models.

5.3 Genetic Correlations

5.3.1 Phenotypic Correlations

Phenotypic correlations between parities within traits were in all cases very weak. Phenotypic correlations between traits were all in line with the genetic correlations but in general a little weaker. Similarly, phenotypic correlations between fertility traits and yield traits were almost all in line with the genetic correlations but in general a little weaker.

5.3.2 Genetic Correlations Between Parities Within Traits

Estimated genetic correlations between the performance of heifers and cows within traits had a wide range from weak to strong. These results were similar to other studies in the way that they indicate that heifer fertility and cow fertility should not be considered the same trait since correlations were far from one (Liu et al., 2017; Muuttoranta et al., 2019; Roxström et al., 2001; Tiezzy et al., 2012). Even though genetic correlations between heifer and cow traits were far from one, an improvement in heifer fertility should transfer to an improvement in cow fertility and the other way around. A breeding program should include both heifer and cow fertility traits.

Genetic correlations between CR_{1-3} ranged from weak to strong and thereby differed a little from other studies where correlations were mostly strong (Liu et al., 2017; Muuttoranta et al., 2019; Tiezzy et al., 2012). Genetic correlations between AIS_{1-3} were strong and consistent with other studies (e.g. Eriksson et al., 2017; Liu et al., 2017). However, genetic correlations between IFL_{1-3} ranged from moderate to strong and even though IFL and AIS
should represent the same period, there was a quite a difference in the strength of
correlations between first and third and second and third lactations for IFL and AIS.
Perhaps management choices and other environmental factors are the cause of these
differences which are not seen in other studies where genetic correlations between IFL
traits were strong or very strong (Liu et al., 2017; Muuttoranta et al., 2019; Roxström et al.,
2001; Tiezzy et al., 2012).

ICF\textsubscript{1-3} genetic correlations were very strong between lactations in this study which agrees
with several other studies (e.g. Liu et al., 2017; Muuttoranta et al., 2019; Tiezzy et al.,
2012). In the case of ICL\textsubscript{1-3}, genetic correlations were weakest between ICL\textsubscript{1} and ICL\textsubscript{3}
which was similar to the pattern seen between IFL\textsubscript{1}-IFL\textsubscript{3}. In studies by Liu et al. (2017)
and Roxström et al. (2001) estimated correlations between these traits were mostly in a
similar range as in the current study. Genetic correlations between CI\textsubscript{1-4} were strong or
very strong which is comparable to results by Berry et al. (2013) and Haile-Mariam et al.
(2003).

### 5.3.3 Genetic Correlations Between Fertility Traits

Genetic correlations between the heifer fertility traits were strong, negative between CR\textsubscript{0}
and AIS\textsubscript{0}, and between CR\textsubscript{0} and IFL\textsubscript{0}, and positive between IFL\textsubscript{0} and AIS\textsubscript{0}. Since CR
represents conception at first service, a short IFL period and a low AIS value correspond to
a CR value of 1. IFL\textsubscript{0} and AIS\textsubscript{0} represent the same period after insemination, so a strong
correlation was expected. Other studies showed similar correlations (Liu et al., 2017;
Muuttoranta et al., 2019).

Genetic correlations between CR\textsubscript{c} and AIS\textsubscript{c}, and between CR\textsubscript{c} and IFL\textsubscript{c} were strong but a
little weaker than in the corresponding heifer traits. This might be because to analyse the
cow traits, repeated observations over one, two or three lactations were used, but there was
only one observation for the heifer period. Similar estimates in other studies showed
stronger correlations (Kadarmideen et al., 2003; Liu et al., 2017; Muuttoranta et al., 2019).
Genetic correlations between CR\textsubscript{c} and ICL\textsubscript{c}, and between CR\textsubscript{c} and CI\textsubscript{c} in the current study
were weaker than in studies by Liu et al. (2017) and Kadarmideen et al. (2003). There was
no genetic correlation between CR\textsubscript{c} and ICF\textsubscript{c} in the current study, which might be
management related (maybe farmers generally do not inseminate too early?). The
correlation between CRc and ICFc varies between different studies, and a likely cause is management factors related to when the insemination period starts (Kadarmideen et al., 2003; Liu et al., 2017; Muuttoranta et al., 2019).

The genetic correlation between AISc and ICFc in this study was weak and negative, but still unfavourable and similar to what was found by Kadarmideen et al. (2003), but other studies estimated positive correlations (Liu et al., 2017; Pritchard et al., 2013; VanRaden et al., 2004). On the contrary to the negative (but weak) correlation between AISc and ICFc, the genetic correlation between IFLc and ICFc was positive (but still very weak). The timing of ICF is management related and differs between farms and herds. The IFLc and ICFc correlation differed from other studies where it was stronger (Kadarmideen et al., 2003; Liu et al., 2008; Liu et al., 2017; Muuttoranta et al., 2019). The moderate positive AISc-ICFc and IFLc-ICFc correlations in other studies suggest that cows that have a shorter ICF period also have better fertility in terms of IFL and AIS (Muuttoranta et al., 2019) but this was not observed in the current study. These differences in correlations between the current study and other studies might be related to different breeds, farm management and/or model choices in different studies.

There was a strong genetic correlation between AISc and IFLc which was excepted and agreed with previous estimates (Kadarmideen et al., 2003; Liu et al., 2017). Genetic correlations in the current study between AISc and ICLc, and between AISc and Clc were moderate and lower than estimated correlations in other studies (Kadarmideen et al., 2003; Liu et al., 2017; Pritchard et al., 2013). These correlations were also lower than genetic correlations between IFLc and ICLc, and between IFLc and Clc which is curious since AIS and IFL should represent the same period within ICL and CI. The differences in how these traits were observed might be the cause (the range of AIS was 1-8 inseminations but 0-365 days of IFL). IFLc-ICLc and IFLc-Clc correlations were generally weaker than in other studies, but genetic correlations in this study between ICFc and ICLc, between ICFc and Clc, and between ICLc and Clc were within the range of previous estimates (González-Recio & Alenda, 2005; Kadarmideen et al., 2003; Liu et al., 2008; Liu et al., 2017; Pritchard et al., 2013; VanRaden, et al., 2004).
5.3.4 Genetic Correlations Between Fertility Traits and Yield Traits

The current study used the traits kgMilk and kgProtein within lactation as yield traits (see Material and Methods chapter for a further description). Many other studies use 305-day milk/protein kg within lactations as yield traits. In the text below, those traits are often compared.

The slightly unfavourable genetic correlations between CRc and kgMilkc and between CRc and kgProteinc suggest that high yield does not necessarily imply conception failure at first insemination. In other studies, similar estimates were both lower (Hoekstra et al., 1994; Kadarmideen et al., 2003) and much higher and more unfavourable (Tiezzy et al., 2012). The correlations between CRc and test day yield traits were much weaker than similar estimates in Tiezzy et al. (2012). These indicate differences between management factors (e.g. when to start the insemination period) and differences between breeds (e.g. in milk yield).

Genetic correlations between the fertility traits AISc, IFLc, ICLc and Clc and the yield traits kgMilkc and kgProteinc were moderate, positive and unfavourable. Several other studies show estimates in a similar range between these fertility traits and 305-day milk and/or protein yield (e.g. Eriksson et al., 2017; Pritchard et al., 2013; Sun et al. 2010). In studies by Kadarmideen et al. (2003) and VanRaden et al. (2004), similar estimates of correlations between fertility and production were a little lower than in the current study.

Genetic correlations between the fertility traits AISc, IFLc, ICLc and Clc and the test day yield traits were more unfavourable for TD80 than for TD60. This might indicate that higher yielding cows were inseminated later (closer to TD80). In Sewalem et al. (2008) genetic correlation between IFL and test day milk yield closest to day 90 of the first lactation was lower than similar estimations in the current study. In Tiezzy et al. (2012) estimated correlation between AIS, IFL and ICL and peak milk yield were similar to estimated correlations between those traits and test day traits in the current study.

There were weak or very weak genetic correlations between ICFc and all the yield traits in this study. The previously mentioned management factors of the timing of ICF could explain these weak correlations. In Eriksson et al. (2017) and Kadarmideen et al. (2003)
estimated correlations between ICF and 305-day yield were in a similar range as in the current study but in other studies comparable estimates were higher and more unfavourable (Holtsmark et al., 2008; Pritchard et al., 2013; Sun et al. 2010; Tiezzy et al., 2012). Similar estimates as correlations between ICF and test day traits were higher (unfavourable) in other studies (Sewalem et al., 2008; Tiezzy et al., 2012).

These unfavourable correlations between fertility traits and yield traits indicate that high-yielding cows were 1) inseminated later, 2) took more time to conceive and 3) required more inseminations for each conception than lower-yielding cows. This might indicate that dairy farmers inseminated higher yielding cows later than they otherwise would.

5.4 Estimated Genetic Trends for Fertility Traits

The genetic trends for CR$_{0:3}$ were uneven, quite different between years and showed no clear trends. The levels of mean EBVs seem to be more favourable for heifers and first lactation cows. This could be related to the strain of lactation of second and third lactation cows since they should in general be higher yielding because of on-farm selection.

The positive and unfavourable genetic trends in AIS$_{0:3}$ indicate that the ability of cows to conceive once the insemination period starts, and to stay pregnant has deteriorated during the decade the cows in the dataset were born. A likely cause is the unfavourable genetic correlation observed between AIS and production traits. But perhaps this also indicates that dairy farmers kept trying to inseminate both heifers and cows more often, instead of using natural service bulls after the first insemination failed.

The genetic trends of IFL$_{0:3}$ were not as clearly unfavourable as the trends in AIS$_{0:3}$ even though those traits represented the same process. The way the traits are defined could explain a part of this difference (the range of AIS was 1-8 inseminations but 0-365 days of IFL). The trends for IFL$_{0}$, IFL$_{1}$ and IFL$_{3}$, were slightly unfavourable and indicate that over the decade the data covered it took longer for animals to become pregnant once the insemination period started. The mean EBVs for IFL$_{1}$ and IFL$_{3}$ were overall higher than the other two traits. This suggests dairy farmers were keener to keep younger animals in the herd and tried longer to inseminate first lactation cows. This could also reveal selection
that took place as first lactation cows that did not get pregnant (because of poor fertility) have been culled.

The genetic trends for ICF\textsubscript{1-3} were all negative and favourable. ICF represents the cow’s ability to recover after calving and resume estrous activity but it is also highly influenced by the dairy farmers, as has been previously mentioned. Many factors can affect the decision when to start inseminating cows after calving, e.g. how high yielding the cows is or outlook in the dairy industry. These favourable trends indicate that cows started to cycle sooner because of selection but they may also indicate that farmers adjusted their insemination policy and started inseminating their cows earlier after calving. This could be related to the fact that there are fewer but bigger and possibly more professional farms now than one or two decades ago. Furthermore, the change in housing for the last two decades to free stall barns might be a considerable factor. Another explanation could be better supporting aids in estrous detection. If these favourable trends were indeed mainly influenced by environmental factors, the focus of future studies should be to improve the correction for environmental influence in the estimation of similar genetic trends.

Genetic correlations between ICL and CI suggest that those traits represent the same period, but the genetic trends differed quite a bit (ICL trends were favourable but CI trends were unfavourable). In theory, CI is ICL plus gestation length. A large period of ICL should be ICF (genetic correlation was 0.77) and since there was such a favourable drop in ICF trends, this affected ICL as well. In the dataset about 85-87\% of cows that were inseminated in lactation one, two and three had subsequent calving, so a likely explanation between the different ICL and CI trends is that not all animals that were inseminated had subsequent calving.

The unfavourable genetic trends in CI, the current fertility trait in Iceland, indicate a deterioration in fertility in the cows, specifically a deterioration in the ability to conceive once the insemination period starts (the traits IFL and AIS). A favourable drop can be seen in the CI trends for cows born in 2010 and this drop can also be seen in the trends for ICL and ICF. No clear explanation can be given for this drop. Abnormal data recording could be the cause or AI bulls that had many daughters born in 2010 who showed better fertility than previous years. Perhaps changed perspectives in the dairy industry led to earlier first insemination than previously for cows born in this particular year.
When genetic trends were estimated using models where lactations were repeated measurements, they looked quite similar to the trends estimated with lactations as separate traits within the same traits. Genetic trends for CI, IFL and AIS were generally unfavourable and trends for ICF and ICL were favourable. The favourable drop for animals born in 2010 in the traits CI, ICF and ICL seen in Figure 2 could also be seen in Figure 3.

There has been great genetic progress for production traits in the Icelandic dairy cows for the past decades (Sigurdsson & Jonmundsson, 2011). In the current study, the traits AIS, IFL and CI all had a moderate unfavourable correlation to the traits kgMilk and kgProtein and showed unfavourable genetic trends. This suggests that genetic gain in production traits are partly responsible for the unfavourable genetic trends of these fertility traits.

Sun et al. (2010) showed unfavourable genetic trends in first lactation Danish Holstein for the fertility traits AIS, IFL, ICF, ICL and CI. This differed from the current study where ICF and ICL showed favourable genetic trends. Eriksson et al (2017) showed an unfavourable genetic trend for AIS in first lactation Swedish Red cows but a neutral trend for maiden heifers. For ICF they estimated a neutral or a slightly favourable trend. In the current study, there was very little difference between heifers and cows in genetic trends for AIS.

Phenotypic trends of fertility traits (not shown in the thesis) were much less clear than genetic trends and no conclusion could be drawn from studying them.

5.5 New Genetic Evaluation for Fertility

Fertility currently weighs 10-11% in the total merit index in the breeding program of Icelandic dairy cows and the trait that is used is CI (Eiríksson & Gautason, 2019). Because of recent changes in the breeding program, it is important to consider using another trait to represent fertility to shorten the time it takes to get information about fertility (Eiríksson et al. 2019a; Eiríksson, n.d.).
A conclusion from this study is that fertility of maiden heifers and lactating cows should be considered as separate traits since the correlation between them is not unity and only moderate in some cases. A new genetic evaluation of fertility for Icelandic dairy cows should include a heifer trait which will supply information about daughters of AI bulls earlier than in the current evaluation. Three heifer traits were analysed in the study. CR$_0$ had the highest heritability and because of heavy use of natural service bulls in Iceland (Jóhannesson, 2018; Sigurdsson & Jonmundsson, 2011), it is likely the best heifer trait for now because it does not depend on continued tries to inseminate heifers. A breeding value for CR$_0$ can be obtained about 20-21 months before a breeding value for CI$_{12}$.

The trait ICF had the highest heritability estimates in this study. ICF represents the time it takes for the cow to resume the estrous cycle after calving and is a period within CI, the current fertility trait used. ICF had a strong correlation with CI but information can be collected much sooner. The genetic trends for ICF were favourable, perhaps because of the selection for CI since 1993 or due to farmer influence. ICF is used in fertility evaluations in other countries including Norway and the combined Scandinavian evaluations at NAV (NAV Nordic Cattle Genetic Evaluation, 2019b; Norwegian Red, 2018). It is therefore recommended to include ICF$_{1-3}$ in a new fertility evaluation of the Icelandic cattle.

The most important period within CI is the time it takes for the cow to conceive after being inseminated because in the current study this period had unfavourable genetic trends. It is therefore recommended to include the trait IFL$_{1-3}$ in a new fertility index. The heritability of IFL is comparable to that of AIS, but IFL had a much stronger correlation to CI. Information about IFL can be collected sooner than information about CI for breeding evaluations. IFL should thus have the largest weight in a new fertility index.

In Scandinavia ICF$_{1-3}$ and IFL$_{1-3}$ are evaluated together (with more traits) in a multi-trait model where the first three lactations are separate traits (NAV Nordic Cattle Genetic Evaluation, 2019b). In this study, correlations of traits across lactations were strong or very strong (weaker for IFL than ICF) and different traits should be considered as highly correlated, but genetically separate traits as Muuttontanta et al. (2019) suggest. Therefore, the continued use of a multi-trait model where lactations are considered separate traits is recommended. In the current study, the correlations between ICF$_c$ and IFL$_c$ were very
weak. It may therefore not be necessary to evaluate both traits at the same time in a multi-trait model.

Further studies about the economic values of the suggested traits, ICF, IFL and CR_0, are needed to decide how much weight each trait should be given in a new fertility index. In Scandinavia, all traits in the fertility index are weighted based on their economic value (NAV Nordic Cattle Genetic Evaluation, 2019b). In Norwegian Red bull fertility index, the heifer trait AIS_0 weighs 22% and the cow traits AIS_c and ICF_c each weight 45% and 33%, respectively (Norwegian Red, 2018). The trait that represents the period after insemination until conception (AIS_c) has the highest weight, as I recommend for IFL_{1-3} in a new Icelandic evaluation.

A challenge in evaluating fertility is censored data. Perhaps in a new evaluation, there needs to be a penalty to censored data to reduce bias as was suggested in Liu et al. (2017). This was not done in the current study. Future studies should look at the possibility to estimate breeding values for production traits and fertility traits together in a multi-trait analysis because of the antagonistic relationship between these traits.

5.5.1 Rank Correlations Between Different Fertility Trait EBVs

There were weak correlations between ranking for CR_0 and the other traits. This suggests there will be some re-ranking of sires if CR_0 is included in a fertility index. Rank correlations between EBVs for ICF-CI were moderate for both cows and bulls but a little higher between IFL-CI. ICF and IFL combined make up a large part of CI so because of moderate correlations, some reranking of sires would be expected if ICF and IFL would be used in a new fertility index.

There were very strong correlations between the ranking of both ICF and IFL evaluated with a single-trait model where lactations were repeated measurements and ICF and IFL evaluated with a multi-trait model where lactations were separate traits. These high correlations suggest there will not be much re-ranking of sires depending on the use of a multi-trait model or a model where lactations are repeated measurements in genetic evaluation. Currently, the fertility trait CI is considered a separate trait for three lactations in a multi-trait genetic evaluation.
6 Conclusion

Heritability estimates of female fertility traits in Icelandic dairy cows were all low. Estimates of genetic trends indicated that the ability of cows to conceive after first insemination deteriorated in the decade covered by this study. Traits that represent this period should be emphasised in a new fertility index. A separate trait for heifer fertility should also be included. Heifer fertility and fertility in lactating cows should be considered separate traits in a fertility index. Even though genetic correlations between heifer and cow traits were far from one, an improvement in heifer fertility should transfer to an improvement in cow fertility and the other way around. Performance in different lactations should also be defined as separate, correlated traits. There were generally moderate unfavourable genetic correlations between fertility traits and yield traits which emphasized the importance of improving the genetic evaluation of fertility. If genetic gain for yield continues, it is important to counteract unfavourable trends in fertility. Results suggest there will be some reranking of sires in a new genetic evaluation.

A new fertility index for the breeding evaluation in Icelandic dairy cows should include the heifer trait CR₀ along with the cow traits ICF₁₋₃ and IFL₁₋₃. Further research is needed to determine the weight of new traits in a fertility index.
7 References


http://www.audhumla.is/Frettir/1071/default.aspx


http://www.bondi.is/um-bi/nautastod-bi/


http://citeseerx.ist.psu.edu/viewdoc/download;jsessionid=239E4F5E2E39CF2164C9BAD96900EA01?doi=10.1.1.353.6870&rep=rep1&type=pdf


8 Appendixes

8.1 Appendix I

Table 11 - Heritability estimates for conception rate (CR) in various dairy breeds.

<table>
<thead>
<tr>
<th>Population</th>
<th>h²</th>
<th>CR₀</th>
<th>CR₁</th>
<th>CR₂</th>
<th>CR₃</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irish Holstein-Friesian</td>
<td>0.010</td>
<td>0.010</td>
<td>0.020</td>
<td>Berry et al. (2013)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>The Netherlands</td>
<td>0.014</td>
<td>0.030</td>
<td>0.031</td>
<td>0.033</td>
<td>de Haer et al. (2013)</td>
<td></td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.010</td>
<td>0.014</td>
<td>0.010</td>
<td>0.015</td>
<td>Liu et al. (2017)</td>
<td></td>
</tr>
<tr>
<td>Scandinavian Holstein</td>
<td>0.008</td>
<td>0.025</td>
<td>0.030</td>
<td>0.029</td>
<td>Muuttoranta et al. (2019)</td>
<td></td>
</tr>
<tr>
<td>Scandinavian RDC</td>
<td>0.017</td>
<td>0.017</td>
<td>0.021</td>
<td>0.024</td>
<td>Muuttoranta et al. (2019)</td>
<td></td>
</tr>
<tr>
<td>Italian Brown Swiss</td>
<td>0.020</td>
<td>0.030</td>
<td>0.032</td>
<td>Tiezzy et al. (2012)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td>0.040</td>
<td></td>
<td></td>
<td></td>
<td>González-Recio &amp; Alenda (2005)</td>
<td></td>
</tr>
<tr>
<td>UK</td>
<td>0.016</td>
<td></td>
<td></td>
<td></td>
<td>Kadarmideen et al. (2003)</td>
<td></td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.012</td>
<td></td>
<td></td>
<td></td>
<td>Liu et al. (2017)</td>
<td></td>
</tr>
</tbody>
</table>

Subscript defines heifer traits as 0 and lactations as 1, 2 and 3 respectively. h² estimates in italics include multiple lactations. The definition of conception rate can vary between studies.

Table 12 - Heritability estimates for number of inseminations per service period (AIS) in various dairy breeds.

<table>
<thead>
<tr>
<th>Population</th>
<th>AIS₀</th>
<th>AIS₁</th>
<th>AIS₂</th>
<th>AIS₃</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irish Holstein-Friesian</td>
<td>0.030</td>
<td>0.040</td>
<td>0.040</td>
<td>Berry et al. (2013)</td>
<td></td>
</tr>
<tr>
<td>Swedish Red</td>
<td>0.021</td>
<td>0.029</td>
<td>0.03</td>
<td>Eriksson et al. (2017)</td>
<td></td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.013</td>
<td>0.029</td>
<td>0.027</td>
<td>0.027</td>
<td>Liu et al. (2017)</td>
</tr>
<tr>
<td>Swedish Red and White</td>
<td>0.024</td>
<td>0.028</td>
<td>0.030</td>
<td>0.021</td>
<td>Roxström et al. (2001)</td>
</tr>
<tr>
<td>Italian Brown Swiss</td>
<td>0.026</td>
<td>0.046</td>
<td>0.045</td>
<td>Tiezzy et al. (2012)</td>
<td></td>
</tr>
<tr>
<td>Danish Holstein</td>
<td>0.033</td>
<td></td>
<td></td>
<td></td>
<td>Sun et al. (2010)</td>
</tr>
<tr>
<td>Holstein USA</td>
<td>0.018</td>
<td></td>
<td></td>
<td></td>
<td>VanRaden et al. (2004)</td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td>0.020</td>
<td></td>
<td></td>
<td></td>
<td>González-Recio &amp; Alenda (2005)</td>
</tr>
<tr>
<td>UK</td>
<td>0.016</td>
<td></td>
<td></td>
<td></td>
<td>Kadarmideen et al. (2003)</td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.026</td>
<td></td>
<td></td>
<td></td>
<td>Liu et al. (2017)</td>
</tr>
<tr>
<td>Holstein-Friesian UK</td>
<td>0.020</td>
<td></td>
<td></td>
<td></td>
<td>Pritchard et al. (2013)</td>
</tr>
<tr>
<td>Icelandic Dairy Cow</td>
<td>0.070</td>
<td></td>
<td></td>
<td></td>
<td>Ragnarsdóttir (2011)</td>
</tr>
</tbody>
</table>

Subscript defines heifers (0), first, second and third lactation (1, 2, 3, respectively). h² estimates in italics include multiple lactations.
<table>
<thead>
<tr>
<th>Population</th>
<th>h²</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IFL₀</td>
<td>IFL₁</td>
</tr>
<tr>
<td>The Netherlands</td>
<td>0.016</td>
<td>0.032</td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.013</td>
<td>0.034</td>
</tr>
<tr>
<td>Scandinavian Holstein</td>
<td>0.012</td>
<td>0.041</td>
</tr>
<tr>
<td>Scandinavian RDC</td>
<td>0.020</td>
<td>0.024</td>
</tr>
<tr>
<td>Swedish Red and White</td>
<td>0.0169</td>
<td>0.0267</td>
</tr>
<tr>
<td>Italian Brown Swiss</td>
<td>0.017</td>
<td>0.039</td>
</tr>
<tr>
<td>Danish Holstein</td>
<td></td>
<td>0.036</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td>German Holstein</td>
<td>0.014</td>
<td></td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Subscript defines heifers (0), first, second and third lactation (1, 2, 3, respectively). h² estimates in italics include multiple lactations.
<table>
<thead>
<tr>
<th>Population</th>
<th>( h^2 ) ICF₁</th>
<th>( h^2 ) ICF₂</th>
<th>( h^2 ) ICF₃</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irish Holstein-Friesian</td>
<td>0.070</td>
<td>0.040</td>
<td>0.030</td>
<td>Berry et al. (2013)</td>
</tr>
<tr>
<td>The Netherlands</td>
<td>0.082</td>
<td>0.091</td>
<td>0.105</td>
<td>de Haer e. al. (2013)</td>
</tr>
<tr>
<td>Swedish Red</td>
<td>0.035</td>
<td>0.027</td>
<td></td>
<td>Eriksson et al. (2017)</td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.102</td>
<td>0.078</td>
<td>0.069</td>
<td>Liu et al. (2018)</td>
</tr>
<tr>
<td>Scandinavian Holstein</td>
<td>0.057</td>
<td>0.055</td>
<td>0.067</td>
<td>Muuttoranta et al. (2019)</td>
</tr>
<tr>
<td>Scandinavian RDC</td>
<td>0.049</td>
<td>0.025</td>
<td>0.032</td>
<td>Muuttoranta et al. (2019)</td>
</tr>
<tr>
<td>Swedish Red and White</td>
<td>0.027</td>
<td>0.021</td>
<td>0.016</td>
<td>Roxström et al. (2001)</td>
</tr>
<tr>
<td>Italian Brown Swiss</td>
<td>0.142</td>
<td>0.115</td>
<td></td>
<td>Tiezzy et al. (2012)</td>
</tr>
<tr>
<td>Norwegian Red</td>
<td>0.024</td>
<td></td>
<td></td>
<td>Andersen-Ranberg et al. (2005a)</td>
</tr>
<tr>
<td>Norwegian Red</td>
<td>0.050</td>
<td></td>
<td></td>
<td>Holtsmark et al. (2008)</td>
</tr>
<tr>
<td>Danish Holstein</td>
<td>0.087</td>
<td></td>
<td></td>
<td>Sun et al. (2010)</td>
</tr>
<tr>
<td>Holstein USA</td>
<td>0.066</td>
<td></td>
<td></td>
<td>VanRadén et al. (2004)</td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td></td>
<td>0.050</td>
<td></td>
<td>González-Recio &amp; Alenda (2005)</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td></td>
<td>0.063</td>
<td></td>
<td>Gredler &amp; Schnyder (2013)</td>
</tr>
<tr>
<td>German Holstein</td>
<td>0.039</td>
<td></td>
<td></td>
<td>Liu et al. (2008)</td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td>0.083</td>
<td></td>
<td></td>
<td>Liu et al. (2017)</td>
</tr>
<tr>
<td>Holstein-Friesian UK</td>
<td>0.040</td>
<td></td>
<td></td>
<td>Pritchard et al. (2013)</td>
</tr>
<tr>
<td>Icelandic Dairy Cow</td>
<td>0.030</td>
<td></td>
<td></td>
<td>Ragnarsdóttir (2011)</td>
</tr>
</tbody>
</table>

Subscript defines heifers (0), first, second and third lactation (1, 2, 3, respectively). \( h^2 \) estimates in *italics* include multiple lactations.
### Table 15 - Heritability estimates for interval from calving to last insemination (ICL) in various dairy breeds.

<table>
<thead>
<tr>
<th>Population</th>
<th>ICL(_1)</th>
<th>ICL(_2)</th>
<th>ICL(_3)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chinese Holstein</td>
<td>0.049</td>
<td>0.037</td>
<td>0.039</td>
<td>Liu et al. (2018)</td>
</tr>
<tr>
<td>Swedish Red and White</td>
<td>0.037</td>
<td>0.035</td>
<td>0.026</td>
<td>Roxström et al. (2001)</td>
</tr>
<tr>
<td>Italian Brown Swiss</td>
<td>0.093</td>
<td>0.05</td>
<td></td>
<td>Tiezzy et al. (2012)</td>
</tr>
<tr>
<td>Danish Holstein</td>
<td>0.069</td>
<td></td>
<td></td>
<td>Sun et al. (2010)</td>
</tr>
<tr>
<td>Holstein USA</td>
<td>0.040</td>
<td></td>
<td></td>
<td>VanRaden et al. (2004)</td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td></td>
<td>0.040</td>
<td></td>
<td>González-Recio &amp; Alenda (2005)</td>
</tr>
<tr>
<td>German Holstein</td>
<td></td>
<td>0.026</td>
<td></td>
<td>Liu et al. (2008)</td>
</tr>
<tr>
<td>Chinese Holstein</td>
<td></td>
<td>0.041</td>
<td></td>
<td>Liu et al. (2017)</td>
</tr>
<tr>
<td>Icelandic Dairy Cow</td>
<td></td>
<td>0.060</td>
<td></td>
<td>Ragnarsdóttir (2011)</td>
</tr>
</tbody>
</table>

Subscript defines first, second and third lactation (1, 2, 3, respectively). \(h^2\) estimates in *italics* include multiple lactations.

### Table 16 - Heritability estimates for calving interval (CI) in various dairy breeds.

<table>
<thead>
<tr>
<th>Population</th>
<th>CI(_{12})</th>
<th>CI(_{23})</th>
<th>CI(_{34})</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irish Holstein-Friesian</td>
<td>0.030</td>
<td>0.040</td>
<td>0.030</td>
<td>Berry et al. (2013)</td>
</tr>
<tr>
<td>The Netherlands</td>
<td>0.065</td>
<td>0.073</td>
<td>0.080</td>
<td>de Haer et al. (2013)</td>
</tr>
<tr>
<td>Mexican Holstein</td>
<td>0.010</td>
<td>0.020</td>
<td>0.010</td>
<td>Montaldo et al. (2010).</td>
</tr>
<tr>
<td>Danish Holstein</td>
<td>0.070</td>
<td></td>
<td></td>
<td>Sun et al. (2010)</td>
</tr>
<tr>
<td>Spanish Holstein</td>
<td></td>
<td>0.040</td>
<td></td>
<td>González-Recio &amp; Alenda (2005)</td>
</tr>
<tr>
<td>Icelandic Dairy Cow</td>
<td></td>
<td>0.080</td>
<td></td>
<td>Jónmundsson (1980)</td>
</tr>
<tr>
<td>UK</td>
<td></td>
<td>0.025</td>
<td></td>
<td>Kadarmideen et al. (2003)</td>
</tr>
<tr>
<td>Holstein-Friesian UK</td>
<td></td>
<td>0.040</td>
<td></td>
<td>Pritchard et al. (2013)</td>
</tr>
<tr>
<td>Icelandic Dairy Cow</td>
<td></td>
<td>0.021</td>
<td></td>
<td>Ragnarsdóttir (2011)</td>
</tr>
</tbody>
</table>

Subscript defines first, second and third lactation (1, 2, 3, respectively). \(h^2\) estimates in *italics* include multiple lactations.
8.2 Appendix II

Table 17 – Phenotypic averages of yield traits used in the study.

<table>
<thead>
<tr>
<th>Trait$^a$</th>
<th>N</th>
<th>Mean±SD</th>
<th>Min-Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>KgMilk$_c$</td>
<td>69282</td>
<td>5913.5±1794.9</td>
<td>813-16717</td>
</tr>
<tr>
<td>KgProtein$_c$</td>
<td>69282</td>
<td>198.7±58.9</td>
<td>24.9-651.8</td>
</tr>
<tr>
<td>TD60Milk$_c$</td>
<td>66050</td>
<td>24.2±6.88</td>
<td>1.0-60.0</td>
</tr>
<tr>
<td>TD60Protein$_c$</td>
<td>44176</td>
<td>0.74±0.21</td>
<td>0.03-2.5</td>
</tr>
<tr>
<td>TD80Milk$_c$</td>
<td>64964</td>
<td>23.2±6.53</td>
<td>1.0-60.0</td>
</tr>
<tr>
<td>TD80Protein$_c$</td>
<td>43655</td>
<td>0.73±0.20</td>
<td>0.01-2.2</td>
</tr>
</tbody>
</table>

$^a$kgMilk kg of milk over a lactation, kgProtein kg of protein over a lactation, TD60Milk/TD60Protein, TD80Milk/TD80Protein kg of milk/protein on a test day close to day 60/80 of the lactation (range of days are day 50-69 of the lactation for TD60 and day 70-89 of the lactation for TD80).

Figure 4 - Proportion of cows with different number of recorded calvings in the data.
<table>
<thead>
<tr>
<th>Trait</th>
<th>$\sigma^2_a$</th>
<th>$\sigma^2_{pe}$</th>
<th>$\sigma^2_e$</th>
<th>$h^2$ (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>KgMilk</td>
<td>3.61E+05</td>
<td>2.53E+05</td>
<td>8.59E+05</td>
<td>0.245 (0.012)</td>
</tr>
<tr>
<td>KgProtein</td>
<td>365.6</td>
<td>320.3</td>
<td>993.0</td>
<td>0.218 (0.012)</td>
</tr>
<tr>
<td>TD60Milk</td>
<td>3.26</td>
<td>4.22</td>
<td>14.44</td>
<td>0.149 (0.011)</td>
</tr>
<tr>
<td>TD60Protein</td>
<td>0.003</td>
<td>0.004</td>
<td>0.013</td>
<td>0.151 (0.014)</td>
</tr>
<tr>
<td>TD80Milk</td>
<td>3.86</td>
<td>3.78</td>
<td>13.07</td>
<td>0.187 (0.012)</td>
</tr>
<tr>
<td>TD80Protein</td>
<td>0.003</td>
<td>0.004</td>
<td>0.012</td>
<td>0.151 (0.014)</td>
</tr>
</tbody>
</table>

$\sigma^2_a / \sigma^2_{pe} / \sigma^2_e =$ additive genetic variance / permanent environmental variance / residual variance of cow traits using a single-trait model where lactations are repeated measurements (Model 3). $h^2$ estimated heritabilities of cow traits using a single-trait model where lactations are repeated measurements (Model 3).

kgMilk kg of milk over a lactation, kgProtein kg of protein over a lactation, TD60Milk/TD60Protein, TD80Milk/TD80Protein kg of milk/protein on a test day close to day 60/80 of the lactation (range of days are day 50-69 of the lactation for TD60 and day 70-89 of the lactation for TD80).