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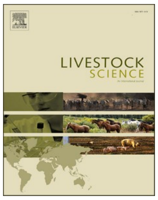

Genetic parameters and genetic trends of female fertility in Icelandic dairy cattle

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HIGHLIGHTS

- Estimated heritabilities for the fertility traits were low, ranging from 0.01 for the trait *interval from first to last insemination* to 0.08 for the trait *interval from calving to first insemination.*
- Genetic correlations between heifer and cow performances within traits ranged from 0.23 to 0.81. Between lactations within traits, the genetic correlations ranged from 0.36 to 1.00
- Genetic correlations between the fertility and production traits were generally unfavourable and estimated genetic trends seemed unfavourable for some fertility traits.
- Heifer and cow fertility traits covering different parts of the reproduction cycle should be included in the genetic evaluation.

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ABSTRACT

Fertility, represented by calving interval, has been included in the genetic evaluation of Icelandic 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 first to last insemination (IFL), interval calving to first insemination (ICF), interval 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 of fertility traits were investigated. Estimated heritabilities for the fertility traits were low, ranging from 0.01 (IFL) to 0.08 (ICF). Genetic correlations between heifer and cow performances within traits ranged from 0.23 to 0.81. Between lactations within traits, the genetic correlations ranged from 0.36 to 1.00. Genetic correlations between different heifer traits were strong, and between different cow fertility traits they 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. 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.

1. Introduction

The Icelandic dairy cow is the only dairy cattle breed in Iceland. It most likely originates from the cattle that the first settlers brought with them, mainly from Norway, when Iceland was colonized in the 9th and 10th century. The breed is believed to have remained mostly isolated

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from other cattle populations since then. Genetic studies have indicated that Icelandic cattle are genetically distinct from other cattle breeds in Western Europe, and closest related to Northern Nordic indigenous cattle breeds. Icelandic dairy cows are therefore unique in terms of their genetic background and history and have remained so partly because of strict regulations of genetic material (Adalsteinsson, 1981; Kantanen, 2000; Gautason et al., 2019). In December 2019 there were 26,415 dairy cows in Iceland (Ráðgjafamiðstöð landbúnaðarins, n.d.-a). During the last two decades, from year 2000 to 2019, the number of dairy farms in Iceland decreased from around 1,000 to 546, whereas the number of animals per farm increased, and the average yield per cow and year increased from just under 4,000 kg to 6,334 kg (Berglund, 2020; Guðmundsson, 2007; Hagþjónusta Landbúnaðarins, 2010; Ráðgjafamiðstöð landbúnaðarins, 2019). In contrast to the rapid increase in milk yield, a deterioration of female fertility has been noticed in Icelandic dairy cattle in recent years (Eiríksson and Gautason, 2019; Sigurdsson and Jonmundsson, 2011), however.

Reproduction has two main functions in dairy cows; to induce the beginning of lactation and to provide replacement animals. Therefore, production and economic efficiency are immensely influenced by reproductive efficiency (Berry et al., 2014; Wathes and Diskin, 2016). Fertility and reproduction problems are among the most common reasons for culling in dairy production (Berglund, 2008). 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, insufficient consideration of fertility traits when selecting for higher milk production has previously been shown to contribute to a decline in reproductive performance in dairy cows (Berry et al., 2014; Walsh et al., 2011; Wathes and Diskin, 2016). The heritability of complex fertility traits is usually less than 5%, mainly because of large influence of management and environmental effects (Berglund, 2008; Berry et al., 2014; Muuttoranta et al., 2019), and to enhance genetic gain fertility traits must be assigned a significant weight in breeding programs.

The current breeding program for dairy cattle in Iceland was adopted in 1993 and fertility, represented by calving interval, has been included in the total merit index since then (Ráðgjafamiðstöð landbúnaðarins, n.d.-b; Sigurdsson and Jonmundsson, 2011). The weight of fertility has been increased from 4% in 2005 to 10% for progeny tested bulls and 11% for cows in the total merit index in 2019 (Eiríksson and Gautason, 2019; Sigurdsson and Jonmundsson, 2011) to counteract decreasing breeding values. Fertility currently is evaluated with a multi-trait animal model where the first three calving intervals are considered separate but correlated traits.

Calving interval captures the cow's ability to recommence normal cyclicity after parturition, express estrous intense enough to be detected and to conceive and establish pregnancy. The strength of calving interval is that two calving dates are an obvious measurement much less affected by the quality of data than other fertility measures. The weakness is that the cow must calve twice for information to be collected and information is not available for cows that are culled before subsequent calving (Berry et al., 2014; Tiezzy et al., 2011). In 2018 a test day model for milk yield replaced lactation yield in the Icelandic genetic evaluation (Ráðgjafamiðstöð landbúnaðarins, n.d.-b). This has changed the premise for the use of calving interval as a fertility trait because information for genetic evaluation of fertility is now further delayed compared to production records (Eiríksson et al. 2019). The aim of this study was therefore to estimate genetic parameters and genetic trends of different female fertility traits in Icelandic dairy cows and heifers. Such information has been lacking for this breed and is needed to improve the genetic evaluation and thereby counteract further deterioration in fertility.

2. Materials and methods

2.1. Data editing and trait definitions

All data for this study were obtained from the database of the Farmers Association of Iceland. The original data files contained information about 105,162 animals and information about 411,684 artificial inseminations that took place in the years 2008-2018. Only inseminations in the first three lactations and inseminations of maiden heifers were included. The pedigree file was built using a sire-dam structure. The statistical software SAS 9.4 (SAS Institute, 2013) was used in basic data handling. The pedigree was traced back 10 generations and pruned for non-informative animals. There were 129,768 individuals in the final pedigree file.

The analysed traits were: Conception rate at first insemination (CR), number of inseminations per service period (AIS), interval from first to last insemination in days (IFL), interval from calving to first insemination in days (ICF), interval from calving to last insemination in days (ICL), calving interval in days (CI). Dates of birth, inseminations, calvings, and culling were used to define the fertility traits: $AIS_{0,\ 1,\ 2,\ 3}$, $CR_{0,\ 1,\ 2,\ 3}$, $IFL_{0,1,\ 2,\ 3}$, $ICF_{1,\ 2,\ 3}$, $ICL_{1,\ 2,\ 3}$, and $CI_{12,\ 23,\ 34}$, (Subscripts define lactations 1-3, and 0 is used for maiden heifers. In the case of CI, subscript defines an interval between two calvings). Later in this text, C as a subscript defines a cow trait for which lactations are treated as repeated measurements. Other traits defined from information in the available data were: lifespan, number of recorded calvings, interval from last insemination to calving (gestation length), age at first insemination (AFI), and age at first calving (AFC). Lactation numbers were defined based on calving dates. Inseminations within each lactation were counted for the $AIS_{0\text{-}3}$ traits. CR was defined in a way that if $IFL_{0\text{-}3}$ was in the interval 0-4 days and the animal calved 260-302 days later, then $CR_{0\text{-}3}$ was set to 1 (success). If $IFL_{0\text{-}3}$ was 5 days or more and the animal calved 260-302 days later then $CR_{0\text{-}3}$ was set to 0 (failure). If the animal was inseminated at least once and did not calve then $CR_{0\text{-}3}$ was also 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 records with specific comments about any insemination, such as "*Cow not in estrous*", "*Synchronized*" or "*Cow already pregnant*", were also deleted. 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, and only animals in Herd-Year classes with a minimum of 3 animals were included. After data editing, 52,951 cows with insemination records remained.

Available information from the Farmers Association of Iceland 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. The milk and protein yield traits kgMilk and kgProtein per lactation, TD60Milk and TD60Protein at test day 60, and TD80Milk and TD80Protein at test day 80 were extracted and used for further analyses. The data file containing lactation yield was already edited according to most of the standard procedures for the routine 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 required to be between 1 kg and 60kg in the study, which is similar to the editing done for the routine genetic evaluation.

2.2. Statistical models and analyses

(Co)variance components were estimated using the AI-algorithm in the DMU-package (Madsen and Jensen, 2013). Most of the analysed female fertility traits in this study have not previously been included in the Icelandic cattle genetic evaluation, and it was therefore of interest to study the feasibility of using models of different levels of complexity. This is the rationale behind the different types of models presented below, including both single-trait and multiple-trait models. In addition, the number of traits in multi-trait analyses were restricted due to computational limitations. In total five different linear models (Models 1-5 below) were used, including both models treating different lactations as different traits (Model 1 and 2), as well as repeatability models (Models 3-5). The decision on which fixed effects to include in the models was based on literature, the current routine genetic evaluation, tests of significance of different effects using PROC MIXED in SAS (SAS Institute, 2013), along with trial runs of variance component estimations using different models in DMU (Madsen and Jensen, 2013). For example, the effect of service sire was included in preliminary analyses of the trait conception rate at first service but because it had very little impact on the results, it was not included in the final analyses. The DMU-package (DMU5 option) was also used for estimation of breeding values for investigation of genetic trends. Models 1 and 2 were used for this purpose, and only breeding values for cows with own observation for each trait were plotted in figures.

In the below models y_i is the vector of the trait observation, β_i is the vector of fixed effects for the ith trait, a_i is the vector of random additive genetic effects for the ith trait, pe_i is the vector of permanent environmental effects for the ith trait (Models 3, 4 and 5), e_i is the vector of random residual effects for the ith trait. X_i, Z_i and W_i were the incidence matrices connecting β_i, a_i and pe_i to y_i. Fixed effects used in the models were *herd × calving year, age at calving (months)* and *insemination year × month.* For heifer traits *herd × birth year* and *age at first insemination (months)* was instead used in addition to *insemination year × month. AI technician* was an additional fixed effect in CR models for both heifer and cow traits. For CI, kgMilk, kgProtein, and TD traits *calving month* was used instead of *insemination year × month.* Models for TD traits also included the effect of *Test day (no. of days milking)*. In addition, lactation length was included as a regression in kgMilk and kgProtein models.

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 $e \sim N(0, I \otimes R_a)$, where A was the additive 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 in the estimations by using a built-in option in DMU.

Multi-trait models were used to analyse covariances between lactations within the same trait. For traits defined in both heifers and cows ($AIS_{0\text{-}3}$, $CR_{0\text{-}3}$, $IFL_{0\text{-}3}$), a four-trait model (Model 1) was used, where y_i is the vector of observations ($i = 0, 1, 2, 3$ representing heifers (0) and lactations 1, 2 and 3).

$$\begin{bmatrix} y_0 \\ y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_0 & 0 & 0 & 0 \\ 0 & X_1 & 0 & 0 \\ 0 & 0 & X_2 & 0 \\ 0 & 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} \beta_0 \\ \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} Z_0 & 0 & 0 & 0 \\ 0 & Z_1 & 0 & 0 \\ 0 & 0 & Z_2 & 0 \\ 0 & 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} \alpha_0 \\ \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} e_0 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} \tag{1}$$

A three-trait model (Model 2) was used for traits only defined in cows ($ICF_{1\text{-}3}$, $ICL_{1\text{-}3}$,

$CI_{1\text{-}4}$). A three-trait model was also used to estimate correlations between the three heifer traits (AIS_0, IFL_0, CR_0.). In Model 2, y_i is the vector of observations ($i = 1, 2, 3$ representing fertility traits 1, 2 and 3).

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix} \tag{2}$$

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

$$y = X\beta + Z\alpha + Wpe + e \tag{3}$$

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, where y_i is the vector of observations ($i = 1, 2$ representing fertility traits 1 and 2).

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} pe_1 \\ pe_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \tag{4}$$

To estimate correlations between a fertility trait and two yield traits (milk and protein yield) a three-trait model (Model 5) was used, in which multiple lactations were treated as repeated measurements. In Model 5, y_i is the vector of observations ($i = 1$ representing a fertility trait and 2, 3 the yield traits).

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} W_1 & 0 & 0 \\ 0 & W_2 & 0 \\ 0 & 0 & W_3 \end{bmatrix} \begin{bmatrix} pe_1 \\ pe_2 \\ pe_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix} \tag{5}$$

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 and Jensen, 2013) using Taylor series expansion as was described in Albertsdóttir et al. (2007).

3. Results

Phenotypic averages of the six fertility traits analysed are presented in Table 1. Average phenotypic values for AIS and CR were more favourable for heifers than for cows. CR was least favourable in the third lactation. Average phenotypic values for AIS, IFL, ICF, ICL and CI were

Table 1
Phenotypic averages of female fertility traits in the Icelandic dairy cow.

Trait[a]	N	Mean ± SD	Min–Max
CR_0	27236	0.62 ± 0.48	0–1
CR_1	42871	0.51 ± 0.50	0–1
CR_2	26044	0.52 ± 0.50	0–1
CR_3	14860	0.50 ± 0.50	0–1
AIS_0	27236	1.57 ± 0.99	1–8
AIS_1	42871	1.78 ± 1.15	1–8
AIS_2	26044	1.72 ± 1.11	1–8
AIS_3	14860	1.75 ± 1.14	1–8
IFL_0	27236	25.8 ± 58.5	0–365
IFL_1	42871	25.8 ± 43.8	0–308
IFL_2	26044	24.0 ± 42.1	0–325
IFL_3	14860	24.9 ± 42.5	0–303
ICF_1	42871	82.4 ± 33.8	20–230
ICF_2	26044	79.6 ± 31.9	20–230
ICF_3	14860	80.4 ± 32.0	20–230
ICL_1	42871	108.1 ± 53.3	20–365
ICL_2	26044	103.6 ± 50.5	20–364
ICL_3	14860	105.3 ± 50.9	20–361
CI_{12}	36729	389.8 ± 50.1	286–600
CI_{23}	22632	384.9 ± 46.8	287–599
CI_{34}	12570	386.8 ± 47.4	288–600

[a] *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

more favourable in the second lactation than in the first and the third lactation. Phenotypic averages for the yield traits across lactations are presented in Table 2 to enable comparisons with other breeds.

Variance components and heritability estimates for the fertility traits are shown in Tables 3 and 4. 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 heritability estimates ranged from 0.004 to 0.012 using multi-trait models. For the traits ICF, ICL and CI, the 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 (CR$_c$) to 0.060 (ICF$_c$). Standard errors for the heritability estimates ranged from 0.003 to 0.007 using single-trait models. Table 5 shows the variance components of production traits for comparison. The heritabilities were higher than for the fertility traits and ranged from 0.149 to 0.245.

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, moderate for CR and strong for AIS. Genetic correlations between first and second lactation were strong to very strong in all cases (0.82-0.96) except for CR. 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 (0.01-0.11).

Genetic correlations were strong between all heifer traits, and negative between CR$_0$-AIS$_0$ (-0.98) and CR$_0$-IFL$_0$ (-0.90), and positive between AIS$_0$ and IFL$_0$ (0.87). Corresponding phenotypic correlations were moderate or strong between all traits (-0.67, -0.56 and 0.73, respectively). 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 7. Strong negative genetic correlations were estimated between CR$_c$ and -AIS$_c$ as well as CR$_c$- and IFL$_c$, and moderate negative genetic correlations between CR$_c$ and -ICL$_c$ as well as between CR$_c$ and -CI$_c$ (ranging from -0.57 to -0.81). Very strong positive genetic correlations were found between IFL$_c$ and AIS$_c$ and also between ICL$_c$ and CI$_c$ (0.94 to 0.97). Genetic correlations between ICF$_c$ and the traits CR$_c$, AIS$_c$ and IFL$_c$ were weak (ranging from -0.17 to 0.09).

Genetic correlations between the six fertility traits and the different production traits using a three-trait model where lactations were treated as repeated measurements (Model 5) are shown in Table 8. Estimated genetic correlations with production (kgMilk$_c$ and kgProtein$_c$) were moderate for AIS$_c$, IFL$_c$, ICL$_c$ and CI$_c$ (0.41-0.53) and weak for CR$_c$ (-0.19 to -0.22) and ICF$_c$ (0.16-0.22). Genetic correlations with TD60Milk and TD60Protein were weak for AIS$_c$, IFL$_c$, ICL$_c$ and CI$_c$ (0.20-0.29) and very weak for CR$_c$ and ICF$_c$ (0.00-0.09). Genetic correlations between TD80Milk and TD80Protein were very weak for CR$_c$ and ICF$_c$ (-0.10-0.18) and weak to moderate for AIS$_c$, IFL$_c$, ICL$_c$ and CI$_c$ (0.33-0.43).

Table 2
Phenotypic averages of production traits in the Icelandic dairy cow.

Trait[a]	N	Mean ± SD	Min–Max
KgMilk$_c$	69282	5913.5 ± 1795	813–16717
KgProtein$_c$	69282	198.7 ± 58.9	24.9–651.8
TD60Milk$_c$	66050	24.2 ± 6.88	1.0–60.0
TD60Protein$_c$	44176	0.74 ± 0.21	0.03–2.5
TD80Milk$_c$	64964	23.2 ± 6.53	1.0–60.0
TD80Protein$_c$	43655	0.73 ± 0.20	0.01–2.2

[a] *kgMilk* kg of milk per lactation, *kgProtein* kg of protein per 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).

Table 3
Variance components[a] of fertility traits using multi-trait models

Trait[b]	σ^2_a	σ^2_e	h² (SE)
CR$_0$	3.44 E-03	0.210	**0.016** (0.005)
CR$_1$	4.81 E-03	0.231	**0.020** (0.005)
CR$_2$	4.91 E-03	0.230	**0.021** (0.006)
CR$_3$	6.49 E-03	0.234	**0.027** (0.010)
AIS$_0$	0.012	0.864	**0.014** (0.005)
AIS$_1$	0.024	1.177	**0.020** (0.004)
AIS$_2$	0.027	1.111	**0.024** (0.007)
AIS$_3$	0.023	1.202	**0.019** (0.008)
IFL$_0$	30.8	3101.3	**0.010** (0.005)
IFL$_1$	43.5	1731.8	**0.025** (0.005)
IFL$_2$	28.2	1632.1	**0.017** (0.006)
IFL$_3$	43.2	1700.0	**0.025** (0.010)
ICF$_1$	37.7	652.0	**0.055** (0.008)
ICF$_2$	57.6	653.7	**0.081** (0.012)
ICF$_3$	32.2	705.7	**0.044** (0.011)
ICL$_1$	78.8	2225.3	**0.034** (0.006)
ICL$_2$	93.7	2118.0	**0.042** (0.009)
ICL$_3$	60.7	2236.4	**0.026** (0.010)
CI$_{12}$	77.3	2038.2	**0.037** (0.007)
CI$_{23}$	80.1	1870.0	**0.041** (0.009)
CI$_{34}$	37.4	2012.5	**0.018** (0.010)

[a] σ^2_a / σ^2_e = additive genetic variance / residual variance using multi-trait models (Model 1 and 2), h² = estimated heritability.

[b] *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 4
Variance components[a] for fertility traits using single-trait models.

Trait[b]	σ^2_a	σ^2_{pe}	σ^2_e	h² (SE)
CR$_c$	4.13E-03	4.90E-03	0.228	**0.017** (0.003)
AIS$_c$	0.024	0.064	1.103	**0.020** (0.004)
IFL$_c$	35.9	66.6	1647.8	**0.021** (0.004)
ICF$_c$	43.5	26.7	631.8	**0.060** (0.007)
ICL$_c$	78.5	113.8	2116.7	**0.034** (0.005)
CI$_c$	77.8	105.6	1912.5	**0.037** (0.005)

[a] σ^2_a/ σ^2_{pe} / σ^2_e = additive genetic variance / permanent environmental variance / residual variance of a cow trait using a single-trait model where lactations were repeated measurements (Model 3). h² = estimated heritability of a cow traits using a single-trait model where lactations were repeated measurements (Model 3).

[b] *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 5
Variance components[a] for production traits using single-trait models.

Trait[b]	σ^2_a	σ^2_{pe}	σ^2_e	h² (SE)
KgMilk$_c$	3.61E+05	2.53E+05	8.59E+05	**0.245** (0.012)
KgProtein$_c$	365.6	320.3	993.0	**0.218** (0.012)
TD60Milk$_c$	3.26	4.22	14.44	**0.149** (0.011)
TD60Protein$_c$	0.003	0.004	0.013	**0.151** (0.014)
TD80Milk$_c$	3.86	3.78	13.07	**0.187** (0.012)
TD80Protein$_c$	0.003	0.004	0.012	**0.151** (0.014)

[a] σ^2_a/ σ^2_{pe} / σ^2_e = additive genetic variance / permanent environmental variance / residual

[b] *kgMilk* kg of milk per lactation, *kgProtein* kg of protein per 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).

Estimated genetic trends in genetic standard deviation units for fertility traits and for kgMilk$_c$- and kgProtein$_c$ are shown in Fig. 1. The traits CR$_{1\text{-}3}$ showed no clear trends during the studied period (not

Table 6
Genetic correlations[a] between fertility traits in different parities using a multi-trait model (Model 1 and 2).

Trait[b]	r_{a0a1}	r_{a0a2}	r_{a0a3}	r_{a1a2}	r_{a1a3}	r_{a2a3}
CR	0.60	0.44	0.40	0.36	0.37	0.91
AIS	0.64	0.81	0.74	0.82	0.86	0.99
IFL	0.35	0.44	0.23	0.82	0.52	0.79
ICF				0.96	0.95	0.88
ICL				0.85	0.60	0.93
CI				0.86	0.81	~1.00

[a] r_{aiaj} = genetic correlation within a trait between parities i and j.

[b] *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.

Phenotypic correlations ranged from 0.01 to 0.11.

SE ranged from 0.13 to 0.28.

Table 7
Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between cow traits using a two-trait model (Model 4).

Trait[a]	$\mathrm{CR_c}$	$\mathrm{AIS_c}$	$\mathrm{IFL_c}$	$\mathrm{ICF_c}$	$\mathrm{ICL_c}$	$\mathrm{CI_c}$
$\mathrm{CR_c}$		-0.81	-0.80	-0.01	-0.57	-0.63
$\mathrm{AIS_c}$	-0.62		0.94	-0.17	0.51	0.56
$\mathrm{IFL_c}$	-0.58	0.81		0.09	0.70	0.87
$\mathrm{ICF_c}$	0.04	-0.06	0.04		0.77	0.82
$\mathrm{ICL_c}$	-0.49	0.67	0.83	0.50		0.97
$\mathrm{CI_c}$	-0.60	0.71	0.90	0.57	0.99	

[a] *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.

shown), whereas $\mathrm{CR_0}$ appeared to be declining although there was much variation in average EBVs between years (Fig. 1). The genetic trends for $\mathrm{AIS_{0\text{-}3}}$ were quite stable and unfavourable. For $\mathrm{IFL_{0\text{-}3}}$ the genetic trends were slightly positive and unfavourable. The genetic trends for $\mathrm{ICF_{1\text{-}3}}$ were clearly negative and favourable. For the $\mathrm{ICL_{1\text{-}3}}$ the genetic trends were slightly negative and favourable. The genetic trends for $\mathrm{CI_{1\text{-}4}}$ were mostly positive and unfavourable but there were some differences between years.

No clear differences in estimated genetic trends were seen for the cow fertility traits when evaluated together with yield traits in Model 5 compared with when evaluated as single traits in Model 3 (Fig. 1). However, the estimated genetic variance, and consequently the heritability, was slightly higher for fertility traits when analysed together with yield traits. For example, the heritability estimate increased with 2% ($\mathrm{ICF_c}$) – 9% ($\mathrm{AIS_c}$) when analysed together with $\mathrm{kgMilk_c}$ and $\mathrm{kgProtein_c}$.

4. Discussion

The challenge of breeding for fertility lies in the collection of large amounts of data of sufficient quality. Generally, fertility traits are based on calving and insemination data, and each trait is influenced by management and has its weaknesses and strengths (Berglund, 2008). This is the most extensive study done on female fertility in Icelandic cattle in terms of number of analysed fertility traits and data size. Fertility currently weighs 10-11% in the total merit index in the breeding program of Icelandic dairy cows and CI is the only trait that is used today (Eiríksson and Gautason, 2019). Because of recent changes in the breeding program, it is important to consider using other traits to represent fertility to shorten the time it takes to get information (Eiríksson et al. 2019). Genetic gain in an economically essential trait like fertility is especially important in the relatively small Icelandic dairy cow breed, which has a unique genetic background compared to most other European commercial breeds, to ensure that it will remain commercially competitive and viable (Gautason et al., 2019).

4.1. Phenotypic values

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 in lactating cows shows their ability to conceive when they are under the metabolic load of lactation and can therefore be more negatively influenced by increased milk yield (Berglund, 2008; Berry et al., 2014; Tiezzy et al. 2012).

In the present study, phenotypic values for CR and AIS were more favourable for heifers than for cows, which suggests that heifers needed on average fewer inseminations to conceive. Even though AIS and IFL should represent the same period in the fertility cycle, the average phenotypic values of IFL were instead more favourable for second and third lactation than for heifers and first lactation cows. These differences may at least partly be due to farm management related factors, for example missed estrous detection of heifers for one cycle, which might affect the observation of the traits.

It should be noted that the average level of milk production in the Icelandic cow is more comparable with e.g. that of the related native Swedish Polled Cattle (SKB), than with the large commercial breeds (Växa Sverige, 2020). It is possible that the relatively low yield levels may influence the impact of milk production on fertility in the Icelandic cows, in accordance with the resource allocation theory described for dairy cattle by Rauw et al. (1998). However, the body size of the Icelandic cow is smaller (450-500 kg) than in the common commercial breeds (Sigurdsson and Jonmundsson, 2011) and it is likely that the feed intake and available energy for production and fertility is also lower. When instead comparing phenotypic averages for the female fertility traits with the Swedish Polled Cattle, the current breeding goal trait CI is somewhat lower in the Icelandic cattle, whereas the AIS per service

Table 8
Genetic correlations between fertility traits and yield traits using a three-trait model (Model 5). (Phenotypic correlations in parentheses).

Trait[a]	$\mathrm{kgMilk_c}$	$\mathrm{kgProtein_c}$	$\mathrm{TD60Milk_c}$	$\mathrm{TD60Protein_c}$	$\mathrm{TD80Milk_c}$	$\mathrm{TD80Protein_c}$
$\mathrm{CR_c}$	-0.22 (-0.13)	-0.19 (-0.14)	0.08 (0.03)	0.04 (0.03)	-0.10 (0.03)	-0.09 (0.03)
$\mathrm{AIS_c}$	0.43 (0.19)	0.41 (0.20)	0.20 (0.06)	0.22 (0.05)	0.35 (0.07)	0.36 (0.07)
$\mathrm{IFL_c}$	0.45 (0.22)	0.44 (0.23)	0.24 (0.05)	0.26 (0.04)	0.36 (0.07)	0.38 (0.06)
$\mathrm{ICF_c}$	0.22 (0.15)	0.16 (0.15)	0.09 (0.03)	-0.00 (0.02)	0.18 (0.05)	0.08 (0.03)
$\mathrm{ICL_c}$	0.48 (0.33)	0.43 (0.35)	0.25 (0.07)	0.21 (0.05)	0.39 (0.09)	0.34 (0.07)
$\mathrm{CI_c}$	0.53 (0.40)	0.45 (0.41)	0.29 (0.06)	0.21 (0.04)	0.43 (0.08)	0.33 (0.06)

[a] *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.

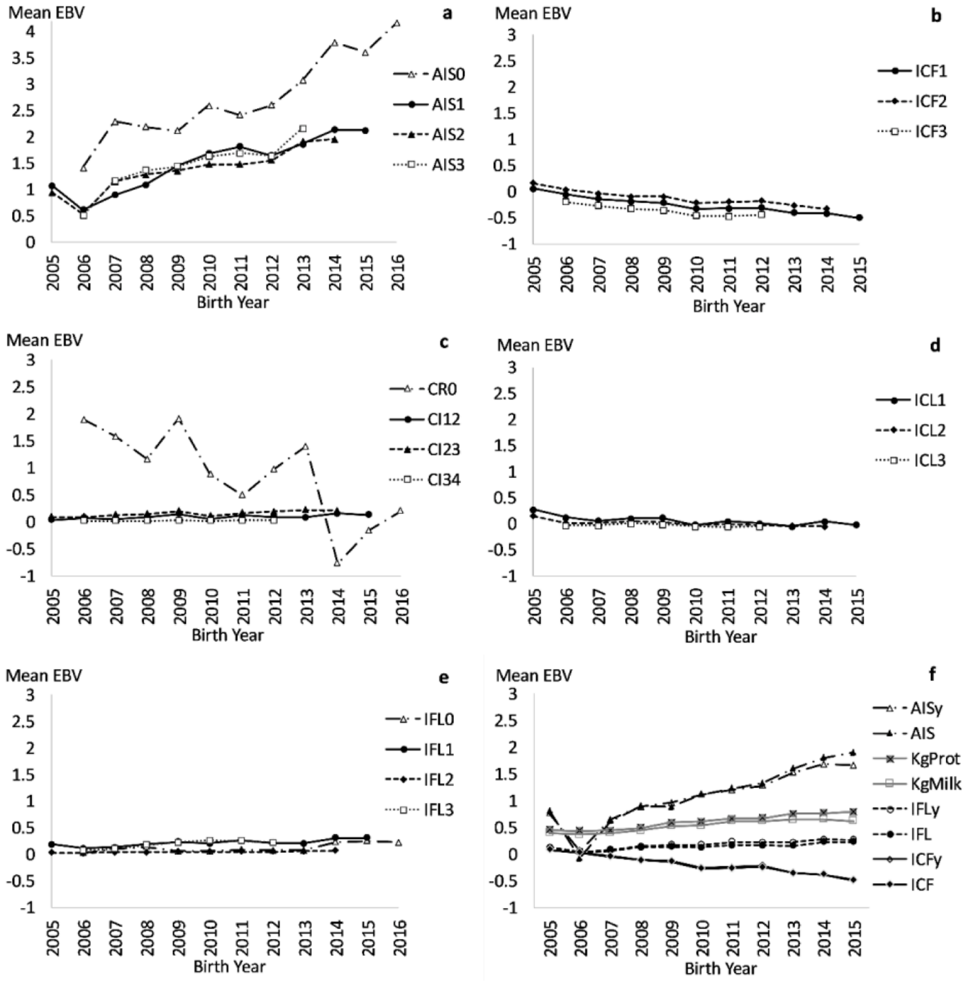

Fig. 1. Genetic trends (mean EBVs in genetic SD units) per birth year for animals with own observations for: a) number of inseminations per service period (AIS) in heifers (0) and cows in lactation 1, 2 and 3, b) interval calving to first insemination (ICF) in lactation 1, 2 and 3, c) conception rate at first insemination in heifers (CR0) and calving interval (CI) between calving 1-2, 2-3 and 3-4, d) interval calving to last insemination (ICL) in lactation 1, 2 and 3, e) interval first to last insemination (IFL) in lactation 1, 2 and 3, f) EBVs estimated treating different lactations as repeated observations for protein yield (KgProt) and milk yield (KgMilk) per lactation, and fertility traits (AIS, IFL and ICF) estimated together with the yield traits above (y) or as single traits. The average values in the beginning and end of each trend generally include fewer EBVs.

period is slightly higher in the Icelandic cattle (Växa Sverige, 2020). In general, when compared with previous reports it seems that the average cow CR, AIS, ICF and IFL were comparable or better in Icelandic cows than in Scandinavian Red breeds and Holstein (Andersen-Ranberg et al., 2005; Eriksson et al., 2017; Muuttoranta et al., 2019). In contrast, the heifer performance in CR and AIS were slightly worse in the current study than in those by Eriksson et al. (2017) and Muuttoranta et al., (2019), stressing the importance of introducing a heifer trait in the Icelandic genetic evaluation.

4.2. *Estimated heritabilities*

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. Heritabilities of CR_{0-3} were similar to estimates given in other studies, as were estimates for ICL_{1-3} (Liu et al., 2017; Muuttoranta et al., 2019; de Haer et al., 2013; Tiezzy et al., 2012). Heritability estimates for AIS_{0-3} and IFL_{0-3} were in a similar range, which could be expected, but in general lower in the current study than what has been presented from other studies (e.g. Eriksson et al., 2017; Liu et al., 2017; Muuttoranta et al., 2019; Tiezzy et al., 2012). However, 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). For this trait, very strong genetic correlations were estimated between lactations, whereas it was less strongly correlated with yield traits than most other fertility traits in the present study. In the current genetic evaluation for Icelandic dairy cattle, it is assumed that heritabilities of CI range from 0.04 to 0.06 (Sigurdsson and Jonmundsson, 2011), which was comparable to the estimates for CI_{12} and CI_{23} in the current study.

4.3. *Genetic correlations between fertility traits*

The estimated genetic correlations between the performance of heifers and cows within traits were far from one an indicate that heifer fertility and cow fertility should not be considered the same trait, as has also been seen in other studies (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 not very strong, they were favourable so that 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 the different heifer fertility traits were strong and similar to estimates in other studies (Liu et al., 2017; Muuttoranta et al., 2019).

The estimated genetic correlations between lactations for the traits AIS, ICF, ICL and CI were also in general consistent with other studies (e.g. Berry et al., 2013; Eriksson et al., 2017; Liu et al., 2017; Muuttoranta et al., 2019; Roxström et al., 2001; Tiezzy et al., 2012). However, genetic correlation between lactations in the traits CR and IFL were weaker in the current study than what had been observed in other studies (Liu et al., 2017; Muuttoranta et al., 2019; Roxström et al., 2001; Tiezzy et al., 2012). It is likely that management choices and other environmental factors are the cause of these differences.

When the cow traits in different lactations instead were treated as repeated observations, the resulting correlations between different fertility traits tended to be somewhat weaker than in previous studies, although some correlations were comparable (Kadarmideen et al., 2003; Liu et al., 2017; Pritchard et al., 2013; VanRaden, et al., 2004). 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), whereas other studies estimated positive correlations (Liu et al., 2017; Pritchard et al., 2013; VanRaden et al., 2004). In contrast to the negative (but weak) correlation between AISc and ICFc in the present study, the genetic correlation between IFLc and ICFc was positive but very weak. The timing of ICF is management related and differs between farms and herds which may influence the results. The correlation between IFLc and ICFc differed from other studies in which it was stronger (Kadarmideen et al., 2003; Liu et al., 2008; Liu et al., 2017; Muuttoranta et al., 2019). The moderate positive correlations between AISc and ICFc, and between IFLc and ICFc, 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 differences between breeds, as well as farm management and/or model choices in the different studies.

4.4. Genetic correlations between fertility and production traits

The only slightly unfavourable genetic correlations between CR_c and $kgMilk_c$ and between CR_c and $kgProtein_c$ suggest that high yield does not necessarily imply conception failure at first insemination. Other studies have presented both weaker (Hoekstra et al., 1994; Kadarmideen et al., 2003) and much more unfavourable (Tiezzy et al., 2012) correlations between these traits. The correlations estimated in the present study between CR_c and test day yield traits were much weaker than similar estimates in Tiezzy et al. (2012). This indicates differences between management factors (e.g., when to start the insemination period) and differences between breeds, e.g. in milk yield levels, as the average yield of Icelandic dairy cows tend to be lower than for the most widely spread commercial cattle breeds in other countries.

Genetic correlations between the fertility traits AIS_c, IFL_c, ICL_c and CI_c and the yield traits $kgMilk_c$ and $kgProtein_c$ 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). Genetic correlations between the fertility traits AIS_c, IFL_c, ICL_c and CI_c and the test day yield traits were stronger for TD80 than for TD60. This might indicate that higher yielding cows were inseminated later (closer to TD80). Sewalem et al. (2010) estimated a stronger genetic correlation between IFL and test day milk yield closest to day 90, whereas the estimates by Tiezzy et al. (2012) between AIS, IFL and ICL and peak milk yield were similar to the estimated correlations between those traits and test day traits in the current study.

There were weak or very weak genetic correlations between ICF_c and all the yield traits in this study. The previously mentioned management factors related to the timing of first insemination after calving may explain these weak correlations. Eriksson et al. (2017) and Kadarmideen et al. (2003) estimated correlations between ICF and 305-day yield in a similar range as in the current study, but in other studies comparable estimates were stronger 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_c and test day traits were more strongly unfavourable in other studies (Sewalem et al., 2008; Tiezzy et al., 2012). Differences between breeds might be a factor, as was mentioned above.

4.5. Genetic trends

There has been great genetic progress for production traits in the Icelandic dairy cows for the past decades (Sigurdsson and Jonmundsson, 2011). In the current study, the traits AIS_c, IFL_c and CI_c all had a moderate unfavourable correlation to the traits $kgMilk_c$ and $kgProtein_c$ 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. The genetic trends for $ICF_{1\text{-}3}$ 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' management choices, as has been previously mentioned. Many factors can affect the decision when to start inseminating cows after calving, for example 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 partly reflect 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, where cows can express estrous behaviour more freely. Another influencing factor could be better supporting aids in estrous detection during the last years. Further studies on the possibilities to improve the correction for such potential environmental influence in the estimation of genetic trends would be useful but may also require more extensive recording.

4.6. Implications for improvement of the genetic evaluation

The results from this study emphasise the importance of improving the current genetic evaluation of fertility in the Icelandic dairy cow to avoid the further deterioration of a vital economic and functional trait. Fertility is of special importance in this relatively small, isolated native breed for which crossbreeding is not an attractive option. Increased economic weights for fertility in terms of CI alone is not sufficient. An improved evaluation should include traits that can be recorded earlier and considers different parts of the reproduction cycle, including both the ability to start cycling again after calving as well as the ability conceive after the insemination period has started. A genetic evaluation of heifer fertility would be beneficial as well because it would speed up the genetic evaluation of AI bulls. Also, according to our results, heifer fertility seems to have a declining genetic trend. This may be due to the fact that the current trait in the genetic evaluation, CI, does not describe the heifer period.

Among the heifer traits analysed in this study, CR_0 had the highest heritability and holds the advantage that it does not depend on continued attempts to inseminate heifers. This is important due to the heavy use of natural service bulls in Iceland (Sigurdsson and Jonmundsson, 2011). We would therefore recommend introducing this heifer trait in the genetic evaluation of Icelandic cattle. The trait ICF had the highest estimated heritability in this study, and it showed a strong correlation with the current breeding goal trait CI. Information can be collected much sooner for ICF than for CI which is a clear advantage. It is therefore recommended to include $ICF_{1\text{-}3}$ in a new fertility evaluation of the Icelandic cattle. It is also important to include a measure of the time it takes for the cow to conceive after being inseminated, because in the current study this period showed unfavourable genetic trends. We therefore recommend to also include the trait $IFL_{1\text{-}3}$ in a new fertility index for Icelandic cattle. The heritability of IFL is comparable to that of AIS, but IFL was much stronger correlated to CI. We recommend the continued use of a multi-trait models where the first three lactations are separate but correlated traits.

Other studies have found that it would be beneficial to analyse fertility traits together with milk production traits (e.g. Sun et al., 2010; Eriksson et al., 2017). In the present study we did not find any noticeable effect on the genetic trends for fertility by including yield traits in a multi-trait model. There was a small increase in the estimated heritability, however. This indicates at least some beneficial effect of using a multi-trait model including also yield. The genetic trend for protein yield per lactation shown in Figure 1 is less than half of the 10% genetic standard deviations per year that was presented for first lactation in Icelandic cattle by Sigurdsson and Jonmundsson (2011). In the present study we used a repeatability model for yield traits, including the first three lactations, and estimated the trend only for cows with own observations of fertility traits, which may explain the difference.

The Farmers Association of Iceland in collaboration with other organizations are in the process of implementing genomic selection in Iceland (Gautason, 2018), and genomic selection could help accelerate improvement especially in low heritability traits like fertility traits and reproduction (Berry et al., 2014). Still, it will be important to include fertility traits that cover different parts of the reproduction cycle, and both heifer and cow fertility.

5. Conclusions

This study showed that fertility in heifers and in lactating cows should be considered separate traits and that heifer fertility should be included in the genetic evaluation of Icelandic dairy cattle. Performance in different lactations should also be defined as separate, but correlated traits. There were generally moderate unfavourable genetic correlations between fertility traits and yield traits, and as expected low heritability values were estimated for fertility. Estimates of genetic trends indicated that the ability of cows to conceive after first insemination deteriorated in the decade covered by this study, therefore an improved genetic evaluation of fertility should focus especially on genetic gain in this period of the reproduction cycle.

Author contribution

Þórdís Þórarinsdóttir: Methodology, **Formal analysis, Data Curation, Writing – Original Draft, Writing – Review and Editing, Supervision, Funding Acquisition. Susanne Eriksson:** Conceptualization, **Writing – Review and Editing,** Supervision. **Elsa Albertsdóttir:** Conceptualization, **Writing – Review and Editing,** Data Curation, Supervision

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the study reported in this paper.

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