BS – ritgerð Maí 2013

Variance Components of litter size in Icelandic farmed mink

(Neovison vison)

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Landbúnaðarháskóli Íslands

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Yfirlýsing Höfundar

Hér með lýsi ég því yfir að ritgerð þessi er byggð á mínum eigin athugunum, er samin af mér og að hún hefur hvorki að hluta né í heild verið lögð fram áður til hærri prófgráðu.

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Kári Gautason

Abstract

An analysis of variance components and a study of pedigree structure was carried out using Icelandic field data. Data from six farms was included, total of 88°928 animals in the pedigree. Two methods were employed, MCMC Gibbs sampler method and REML. The two different methods gave similar results. Heritability (0.03-0.06) and repeatability (0.08-0.16) was lower than in previous studies. EVA software was used to estimate pedigree structure. Average inbreeding was low (0.015). Data suggests that inbreeding is underestimated with the current data recording system. Average inbreeding coefficient decreases after the onset of large scale import of Danish male. The Danish males enter the system as animals from the base population. Full pedigree information should be used for animals if inbreeding is to be controlled. Genetic variance is variable but lower than earlier results. This could be explained by the Bulmer Effect. Phenotypic variance is higher on Icelandic farms than on Danish farms. To ensure optimal calculations of EBV's; these results should be taken into account in the calculations of EBV's. Farmers should be advised to standardize their data recording, count the kits at 3 weeks *post-partum*. Effect of different parameterizations on variance components should be investigated, especially in regard to feed stations.

Key words: mink, Bayesian analysis, REML, heritability, repeatability

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1. Introduction

Litter size is an extremely important economic trait for fur farmers. More kits per female means lower average costs per skin produced. This is because of lower feed costs, less work feeding, breeding and supervising. This is more pronounced as feeding costs and labor costs increase. If skin prices increase, the benefit of having a higher litter size increases (Lagerkvist, 1993). Higher litter size can lead to a substantial benefit from a positive effect on genetic gain as higher selection intensity is possible.

Low litter size has been a problem for Icelandic fur farmers for the last 10-15 years. While farmers have seen a significant gain in other traits of interest, litter size has diminished from a high in the late 1990's (E. E. Einarsson, 2011; Gunnarsson, 2004). Litter size is significantly lower in Iceland compared to Denmark although litter size has not increased significantly in Denmark for the last 5 years as shown in Figure 1 (Hansen & Berg, 2008).

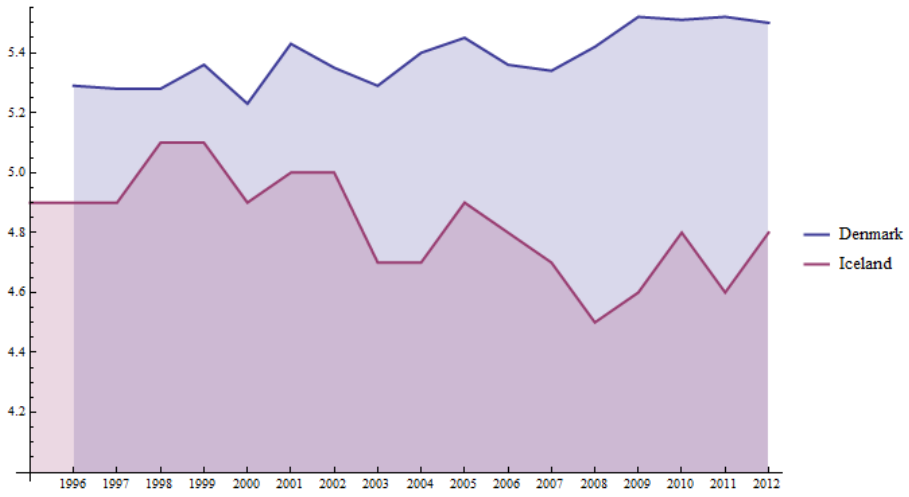

Figure 1. Comparison of average litter size per mated female in Denmark and Iceland

The breeding system in commercially farmed mink differs from what is conventional in traditional animal husbandry. There is no hierarchical breeding structure as in breeding system e.g. in horses and sheep. There is no centralized breeding goal and it is up to each farmer to set his own breeding goal. The breeding goal for skin quality traits can be very different between farmers but for litter size it is much simpler and straight forward.

Farmers in Iceland use an electronic database (FurFarm) to store pedigree information and records from animals. Each animal has a card which follows it from weaning to pelting. Litter size, body weight and skin quality are recorded on the cards and then typed into the database. Litter size, recorded as litter size at pelting, is the economically relevant trait.

The selection criterion for litter size at pelting is litter size recorded at three weeks *post-partum*. It can be considered a complex trait that involves ovulation rate, fertilization rate, prenatal survival rate and pre-weaning survival rate. Litter size recorded at 4 weeks *post-partum* has a higher estimated heritability than litter size at pelting or parturition (Hansen, Su, & Berg, 2010).

Genetic parameters for litter size at 2-4 weeks post-partum in farmed mink have been analyzed on a number of occasions. The range of values found for estimated heritability has varied quite significantly. A value between 0.04 – 0.15 was observed from field data by Hansen, Berg and Jensen in 1999 whereas, earlier analyses based on selection experiments found values of 0.14 – 0.20 (E. J. Einarsson, 1987; Lagerkvist & Lundeheim, 1993). In a recent study, Hansen et al. (2010) found a value of 0.09 at four weeks post-partum. The current model that is used, in the computer program FurFarm to estimate breeding values (BLUP) in mink assumes heritability of 0.09 and repeatability of 0.29.

Breeding values in the FurFarm program are calculated within each farm, within each color type, and if the farmer so chooses, within line. Production year is considered a fixed effect in the current model since there is substantial environmental variation between years. The present method of calculating breeding values, within type and line has been rationalized on the premise that farmers want to be able to pick out the best individuals *within* each color type. However, this is not always the case in practice. Farmers sometimes mix colors in order to improve litter size via heterosis or to improve skin traits. If farmers mix colors systematically there is a little justification for calculating EBV's within color type.

Males have a limited number of offspring since only natural service can be used with mink. This is because of the phenomena of induced ovulation in females and the fact that males only ejaculate during copulation (Hansson, 1947; Venge, 1973). Therefore progeny testing is not used for selection of sires and breeding stocks are maintained within each farm. However, many farmers bring in animals from farmers they believe to have genetically superior animals for one or more traits. Objective comparison of genetic levels between farms is impossible due to usage of within-farm EBV's. Icelandic farmers have systematically brought in breeding

males from Danish farms in the last decade. This has led to a dramatic improvement in skin quality traits as measured by country average auction prices.

Commercial mink farmers usually have few color types with large number of individuals within each type while keeping many color types with few individuals. Based on skin numbers, from Kopenhagen Fur, the average farmer has half his animals in one color type, while the rest is divided unevenly into 10-15 other color types (Dansk Pelsdyravlerforening, 2013). This is potentially an issue for estimation of fixed effects. This could have an effect on the variance component estimation. The current model used for variance component estimation should be reevaluated and different parameterizations tested.

Traditionally, selection has been done by truncation on an index or on a phenotype. A large number of animals (often around 50% of females) are replaced each year and this lowers the selection intensity possible within each generation. The generation interval is shortened however which acts against the lower selection intensity, since generation interval is a fundamental quantity in genetic progress (Falconer, 1989). This is due to rapid advances in skin quality and fluctuation in the market; a dam of three years is often considered "obsolete".

Most farmers in Iceland and Denmark follow a threshold model for selection (Figure 2). An EBV is calculated each year after dams have littered. Based on farmer preference an EBV or phenotype is used to select which animals are going to be weighted and graded in the autumn. Animals that the farmer chooses to cull based on litter size are not considered for breeding, regardless of fur quality or size. A combined selection index is calculated after weighing and grading in the autumn. Each farmer decides economic weights for the combined selection index. It is difficult to optimize economic weights of the selection index as the market for fur is highly volatile, and it is not viable to identify each animal individually in a manner that survives pelting.

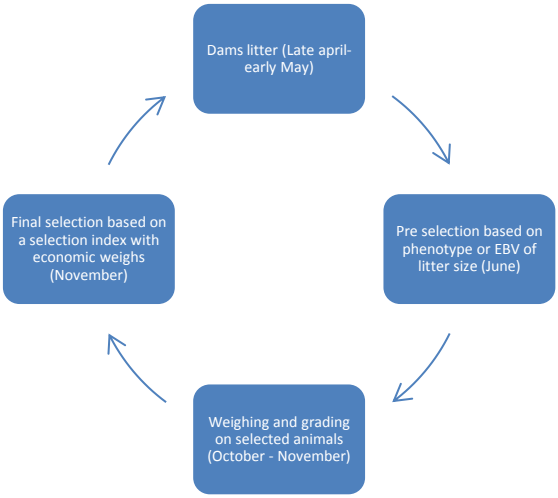

Figure 2. A schematic illustration of the selection of breeding animals in mink

EBV for litter size has been used as basis for selection since the 80's although its use has never been "universal" among commercial fur farmers (Lohi & Berg, 1994). Many farmers have gone back to phenotypes from using the EBV's because they do not trust the EBV's calculated in the FurFarm system (Hansen, 2013). Using selection solely based on phenotype could be a problem in the long term because of the low heritability of litter size and its negative genetic and phenotypic correlation with body size (that has a high estimated heritability). Selection for increased body size could explain the stagnation of litter size in Denmark (Hansen et al., 2010).

Total information available on pedigree is not used in FurFarm as imported animals are considered unrelated to native animals. This can result in unaccounted inbreeding. This can be more severe if related animals are imported repeatedly from the same population. Inbreeding depression in mink has been known to cause reduced fecundity (Demontis et al., 2011). It is possible to use molecular markers to calculate relatedness on a genetic level, but so far this has not been done on Icelandic farmed mink.

The object of this study was to estimate genetic parameters of litter size based on Icelandic field data and to compare them to earlier estimates based on Danish field data that are currently used in prediction of breeding values. A further object was to find out if traditional REML of (co)variance components gave the same result as Bayesian methods. The Bayesian framework adopted makes it possible to make statements about the uncertainty of (co) variance components, which is desirable since the data sets used for analysis are relatively small. In order to make analysis of the data possible, pedigrees had to be built.

2. Material and methods

2.1 Data

The data used in this study were collected from the FurFarm database. A total of six farms were selected to provide the data for the experiment. The selection was based on the premise of number and quality of records. The database is not designed for calculations and therefore records were extracted and edited with the programs SAS® 9.2, Wolfram Mathematica® 9.01 and Microsoft Excel® prior to continuing analysis.

The data from each farm were processed, with the DmuTrace software (Madsen, 2010), to build pedigrees. From these farms, a total of 88°928 individuals were included in the pedigrees. Litter size is (ideally) recorded in the data as kits alive at 3 weeks of age. Summary of the data after processing is presented in Table 1.

Table 1. Characteristics of the data

	Farm					
Item	**1**	**2**	**3**	**4**	**5**	**6**
No. of dams with records	11386	11122	13088	7284	9815	9934
No.of dams with >1 litter	6720	7128	6918	4425	6253	5371
Total number of animals in pedigree	17454	15178	18537	9184	14156	14419
No. of age classes[a]	2	2	2	2	2	2
No. of production years[b]	17	13	17	16	17	14
No. of color types	11	8	9	12	13	8
Average litter size	5.4±3.0	5.1±2.8	4.8±2.9	4.7±2.8	5.7±2.7	5.2±2.9

a: Dams are grouped into yearlings, and dams older than yearlings
b: The number of production years for each farm

2.2 Statistical methods

Variance components were analyzed with two methods, one Frequentist and one Bayesian. REML, as described by (Pattersen & Thompson, 1971) and Markov Chain Monte Carlo *via* the Gibbs sampler, as described by (Jensen, Wang, Sorensen, & Gianola, 1994). The DMU software was used for both methods (Madsen & Jensen, 2007).

2.2.1 Model

A univariate animal repeatability model was assumed.

$$y = Xb + Za + Qc + e$$

Where ***y*** (nx1) is the vector of observations for the trait. **X, Z** and **Q** are matrices relating fixed and random effects to observations. ***b*** (fx1) is the vector of fixed effects, ***a*** *(qx1)* is the vector of random additive genetic values, ***c*** is the vector of random permanent environmental effects. Number of repeated records per dam ranged between 1 and 4. The mode of records was 1 with an average of 1.6 records per female. All farms had similar dispersion of repeated records. Fixed effects are production year, dam age and the animals "type" (color type) which have been known to affect fertility for some color types (Hansen, Berg, & Jensen, 1999). Dams were divided into two groups, based on age, yearling dams and older dams. The number of production years on each farm depended on how long the farmers have used a computerized breeding system. It is necessary to group litters according to production year since there is a random environmental component to litter size that has to be corrected for.

It is assumed that the vector containing observations on litter size (y) is conditionally normally distributed as

$$y|b, a, c, \sigma_e^2 \sim N(Xb + Za + Qc, I\sigma_e^2)$$

Where **I** is an identity matrix of proper order and σ_e^2 is the random residual variance.

It is assumed that additive genetic values and permanent environmental effects are multivariate normally distributed:

$$a|A, \sigma_a^2 \sim N(0, A\sigma_a^2)$$

$$c|\sigma_c^2 \sim N(0, I\sigma_c^2)$$

Where **A** is the numerator relationship matrix, σ_a^2 is the additive genetic variance and σ_c^2 is the permanent environmental variance.

Heritability was calculated as:

$$\frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \sigma_e^2}$$

Repeatability was calculated as:

$$\frac{\sigma_a^2 + \sigma_c^2}{\sigma_a^2 + \sigma_c^2 + \sigma_e^2}$$

2.2.2 Prior distribution of dispersion parameters

For the variance components, a scaled inverse chi square *a priori* distribution was assumed. The prior values were assumed to be 1 for σ_c^2, 0.6 for σ_a^2 and 5.5 for σ_e^2. These are the variance components used in FurFarm in order to calculate breeding values. These priors were used for both the Gibbs sampler and REML analyses. These values were chosen to facilitate convergence. The corresponding degree of belief parameter for the Gibbs sampler (degrees of freedom pretending to the prior distribution) was set to 5, to reflect weak *a priori* information. For **b**, uninformative uniform prior distributions were assumed.

2.2.3 Bayesian analyses

Initially the GIBANAL software was used to estimate burn-in, interleave and chain length (Van Kaam, 1998). Based on these pre-analyses interleave, burn-in and chain length was decided. Interleave was set to 100, to reduce the autocorrelation between saved samples. Burn-in was set to 50,000, and chain length to 500,000.

To monitor convergence, of the Gibbs sampler, effective sample size was calculated according to the method described by (Sørensen, Andersen, Gianola, & Korsgaard, 1995).

Effective sample size is the number of independent samples which delivers the same estimation accuracy as the dependent samples from the Gibbs sampler. When effective sample size approaches the chain length, the samples are drawn independently from the posterior distribution (Sørensen et al., 1995).

There are varying methods to compute effective sample size, in this study the R package coda was used (Plummer, Best, Cowles, & Vines, 2006). Once the samples were obtained estimates of the posterior density functions were made using kernel estimation as implemented in Mathematica 9.01®, i.e. the KernelMixtureDistribution function using the method "Scott". Integration of the estimated function via numerical integration in Mathematica 9.01®. Estimation of variance components, heritability, and repeatability was calculated as the

posterior mean of the samples drawn. Highest posterior density interval was computed using the R package coda to determine the precision of the estimates.

2.2.4 Analysis of pedigree structure

An analysis of the pedigree structure was carried out using the EVA software (Berg, Nielsen, & Sørensen, 2006; Berg, 2012). Two pedigree completeness indices, three and five generations back (PEC3 and PEC5), were estimated. Descriptive statistics were computed for the pedigree, including number of animals per generation, number of inbred animals, average inbreeding coefficients of Wright (1922) and change in average inbreeding coefficients per generation. Average inbreeding was calculated using animals with PEC5 > 0.24, this means that at least both parents were known and at least one grand-parent.

3. Results

The pedigree for Farm 1 had incomplete records so the data from Farm 1 was discarded for further analysis in the study.

3.1 Variance Components

Table 2 shows estimation of variance components with the Bayesian and the REML methods The two methods were in good agreement for permanent environment but Bayesian methods gave in most cases a lower estimate of genetic variance. This lead to a lower point estimates for the Bayesian heritability.

Table 2. Estimation of variance components by Bayesian and REMLmethods. Bayesian estimates are means of the posterior distribution (posterior SE as subscript). Heritability (h^2) has 95% highest posterior density interval as subscript and is based on Bayesian estimates of variance components. REML estimates have asymptotic SE as subscript

	h^2		σ_a^2		σ_c^2	
Farm no	Gibbs	REML	Gibbs	REML	Gibbs	REML
2	$0.05_{0.022 \text{ to } 0.088}$	0.06	$0.40_{0.125}$	$0.47_{0.105}$	$0.74_{0.089}$	$0.73_{0.083}$
3	$0.03_{0.007 \text{ to } 0.0616}$	0.04	$0.26_{0.123}$	$0.32_{0.114}$	$0.47_{0.070}$	$0.48_{0.068}$
4	$0.03_{0.006 \text{ to } 0.048}$	0.03	$0.18_{0.082}$	$0.19_{0.126}$	$0.77_{0.115}$	$0.78_{0.107}$
5	$0.04_{0.017 \text{ to } 0.081}$	0.06	$0.32_{0.124}$	$0.40_{0.108}$	$0.57_{0.078}$	$0.56_{0.076}$
6	$0.03_{0.007 \text{ to } 0.054}$	0.03	$0.23_{0.106}$	$0.22_{0.127}$	$0.47_{0.087}$	$0.47_{0.080}$

3.2 Bayesian analysis

Figure 3 shows the estimated posterior density functions and histograms of the saved samples from the Gibbs sampler. Figure 4 shows cumulative density functions, they show the accumulated posterior probability that heritability has a value equal to or less than the value on the horizontal axis. Table 3 shows the effective sample size of the samples. The effective sample size shows the slow convergence of the estimates.

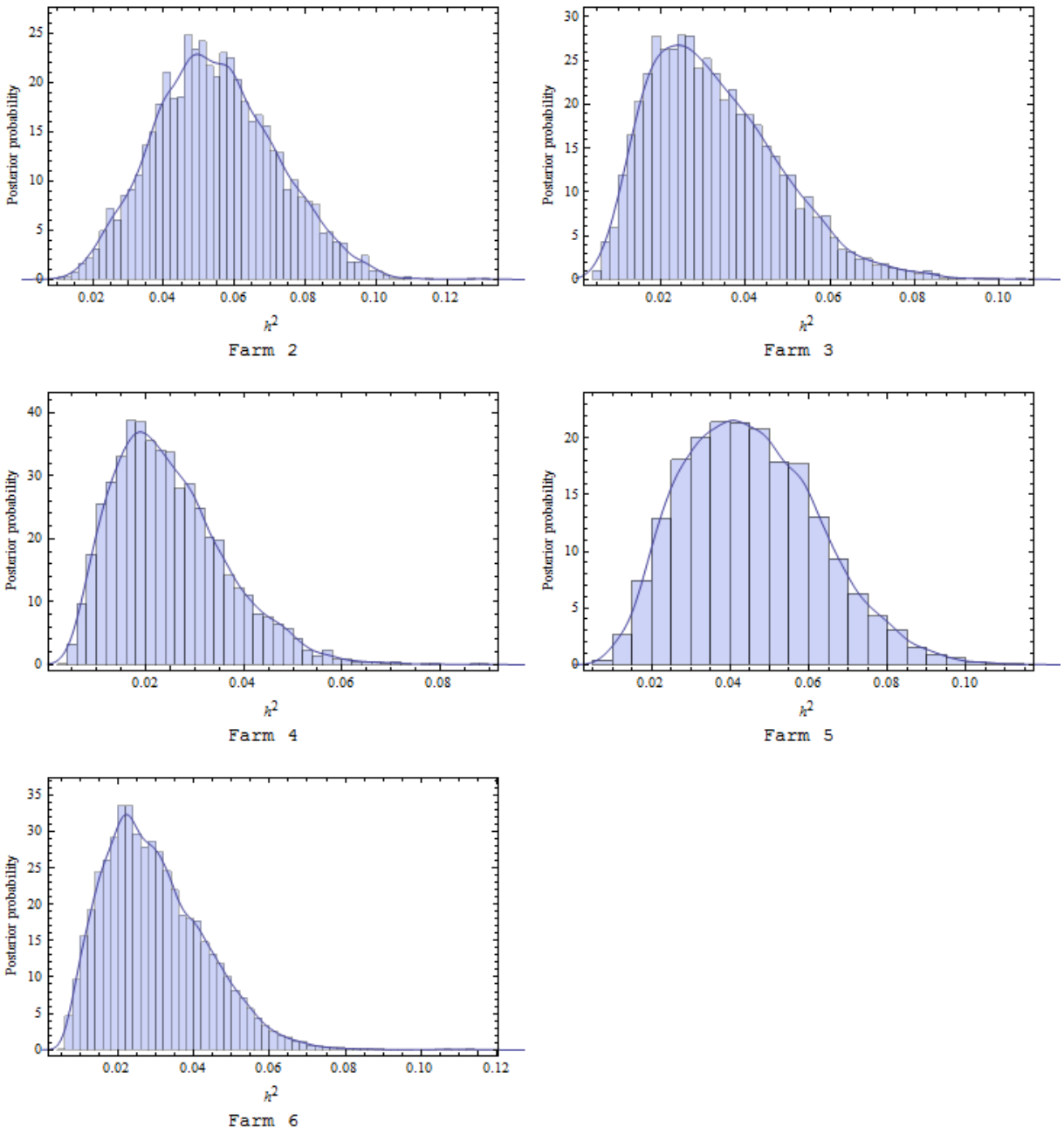

Figure 3. Posterior density function and histogram of heritability.

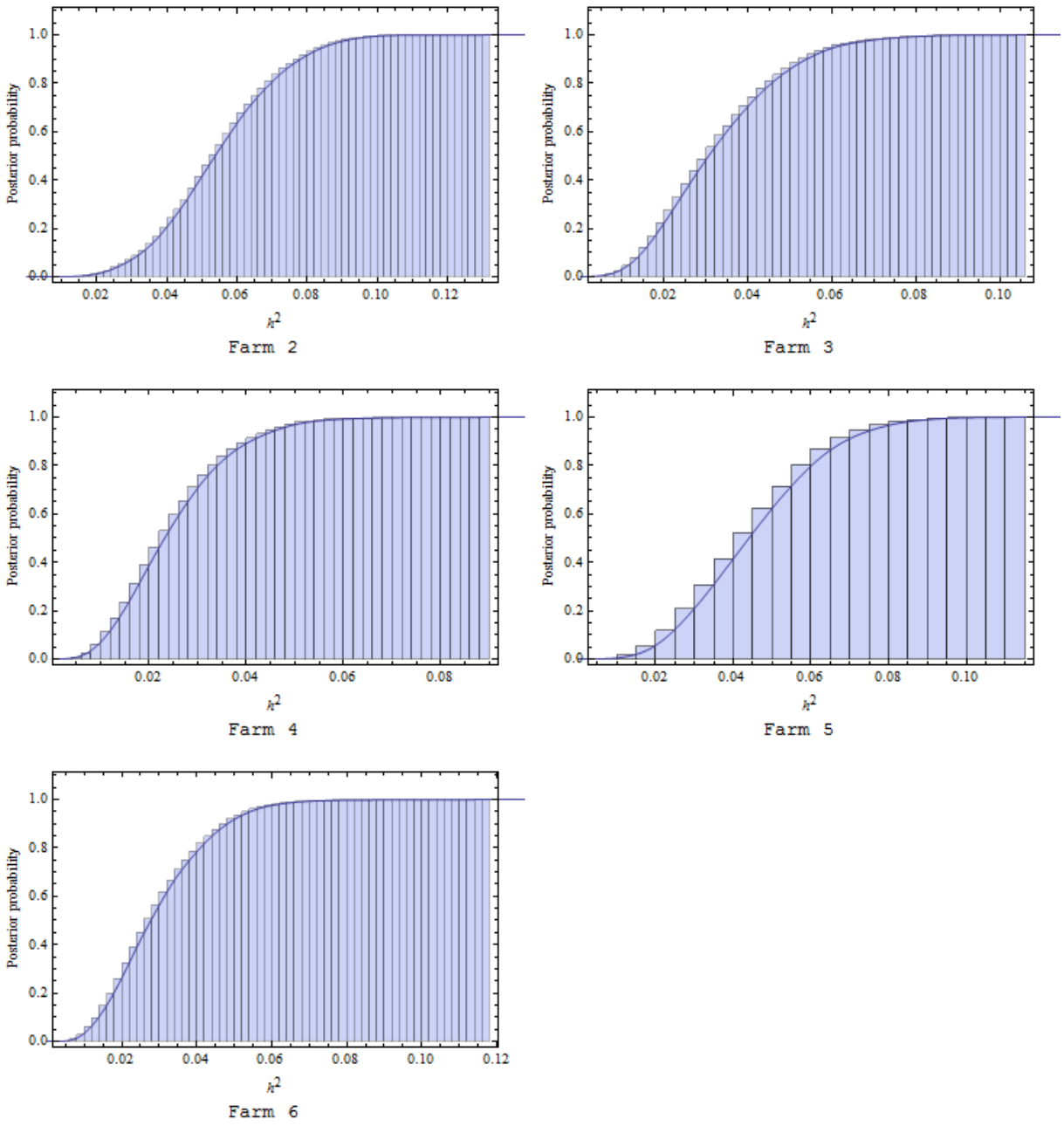

Figure 4. Posterior cumulative distribution function for heritability.

Table 3. Effective sample size as calculated from the Gibbs sampler.

	Farm 2	Farm 3	Farm 4	Farm 5	Farm 6
σ_c^2	1089	820	672	991	269
σ_a^2	398	199	341	367	120
σ_e^2	823	380	1184	629	280
h^2	395	198	338	364	120

3.3 Pedigree Structure

Descriptive statistics for the pedigrees is presented in Table 4. Figure 5 shows level of inbreeding as a function of year of birth.

Table 4. Comparison of pedigree structure between farms.

Farm	No.[a]	No. inbred[b]	avg. F[c]	ΔF[d]	n_e	PEC3[e]	PEC5[f]
2	1588	1072	0.017	0.003	250	0.66	0.55
3	2539	999	0.011	-0.004	139	0.37	0.30
4	618	373	0.018	-0.002	1000	0.50	0.43
5	725	496	0.025	0.003	455	0.60	0.52
6	1415	971	0.0063	-0.002	278	0.66	0.54

a: Number of animals born in 2011 with litters in pedigree
b: Number of animals with inbreeding coefficient≠0
c:Average inbreeding coefficient in the generation (2011)
d: Change in average inbreeding coefficient between animals born in 2010 and 2011
e: Pedigree Completeness Index 3 generations back from last generation (2011)
f: Pedigree Completeness Index 5 generations back from last generation (2011)

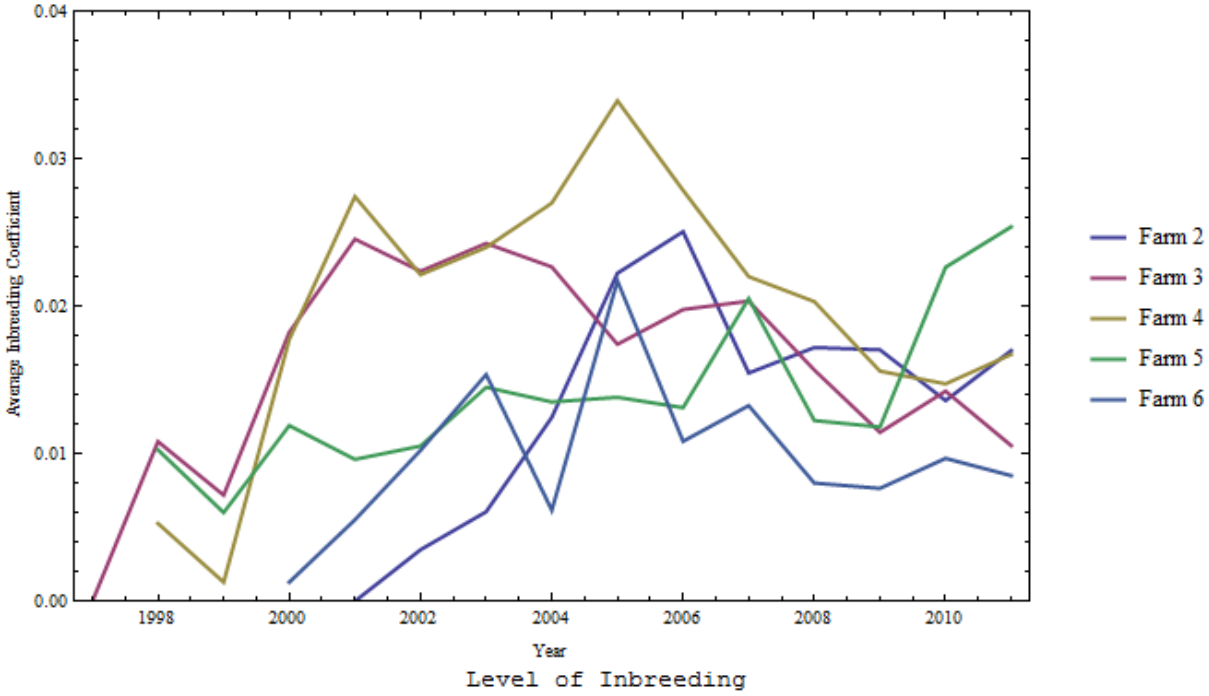

Figure 5. Average inbreeding coefficients per birth year. Data from five farms included. Based on animals with PEC>0.24.

4. Discussion

4.1 Data

Since the data is field data one can assume that litter size was not always recorded at three weeks *post-partum*. This is something that advisors should emphasize to farmers. Standardizing the recording of phenotypes is important to get accurate results.

4.2 Variance Components

An interesting result of this analysis is the permanent environmental and residual variance which was higher in this study compared to the earlier study by Hansen et al (1999). It would seem logical that a major part of this discrepancy is due to the variability of feed quality in Iceland compared to that in Denmark. This could be analyzed using feeding station as a fixed effect in the model. More farms should be included in future analysis as the present study only included 5 farms, that use feed from the 4 feed stations currently operating in Iceland.

4.3 Bayesian Analysis

The diagnostic tools for monitoring convergence showed slow convergence to the posterior distribution for σ_a^2 and σ_c^2. Therefore, a large sampling interval and many iterations where needed to get adequate samples. This is in agreement with (Jensen et al., 1994) which showed that when the genetic variance component is small compared to the total variance the convergence is slow. The highest posterior density intervals gave wide estimates of heritability. For three farms the lower bounds were close to zero. The means of the posterior distributions of genetic variance were slightly lower than the REML estimates. The posterior density functions show a definite deviation from normality (Figure 3). The estimates for heritability and repeatability are lower than earlier studies.

4.4 Pedigree Structure

Both the REML analysis and the mean of the posterior distribution via the Gibbs sampler gave similar results for the variance components. In both cases, the result is a lower genetic variance than reported in earlier studies (E. J. Einarsson, 1987; Hansen et al., 1999; Lagerkvist & Lundeheim, 1993).

Generally, the estimated heritability is similar for both REML and the Gibbs sampler, calculated from the means of the posterior distributions. In some cases, there is a slightly lower value from the Gibbs sampler.

The most likely reason for the lower genetic variance compared to earlier studies, according to the author, is selection. Selection made on parents reduces variance of the offspring. This could be due to selection induced gametic phase disequilibrium, which arises when the population is not in equilibrium under random mating. According to (Falconer, 1989) the rate of this decline is a function of selection intensity. The generation interval in mink is short compared to other species, according to this study around 1.6 years (results not shown). According to the Bulmer effect hypothesis, the genetic variance should be lower on farms who select on a litter index than on farms that use phenotype only. This is mainly due to the higher accuracy of the selection index. The estimated heritability is so low for litter size that truncation on phenotype can be assumed to be only a small deviation from random mating. This is however difficult to test with the current data since there is little knowledge of the selection intensity apart from approximate sector averages.

The Icelandic farms have imported males from Denmark increasingly in the last 10 years. These males make a high genetic contribution in the present population. As little or no information on pedigree follow these males, they are considered unrelated to the animals on the farm. As shown in Table 4 the inbreeding coefficient decreases between years for some farms. That is unusual for farm animals under selection. Normally a decrease in genetic variance due to selection is accounted for in estimated breeding values through the numerator relationship matrix by the inbreeding coefficient of Wright (1922). When the pedigree is not complete, this term is artificially low. As demonstrated in Table 4, the PEC5 is lower than PEC3. Figure 3 shows the average inbreeding coefficient as calculated from animals with

minimal pedigree information, known parents and one grandsire/granddam (PEC>0.24). The trend is clear, as the number of imported animals grows, the average inbreeding coefficient decreases. This is chiefly the result of importation of animals. Farmers do not use animals for breeding that do not have identity cards. If there was no import of animals, the pedigree would be more complete (PEC5 ≈ 1). That is no solution in itself because inbreeding is bound to increase with no import of animals. As demonstrated by Demontis et al. (2011), it is possible to use microsatellite markers to estimate heterozygosity and therefore get an estimation of actual inbreeding. This could be attractive to estimate, since inbreeding is known to reduce performance of mink. Possibly this method could be used when selecting farms to import from. It is known that heterosis has positive results on both litter size and body size (Thirstrup, Larsen, Nielsen, & Pertoldi, 2012). Therefore, it would be potentially of benefit to import from farms that are relatively unrelated to the current population on Icelandic farms.

5. Conclusion

The heritability on Icelandic farms is lower than previously observed in Denmark, Norway and Sweden. This can be due to two reasons, higher environmental variance and/or lower genetic variance. To improve the estimation of breeding values, this should be taken into account in FurFarm. An area of further study for Icelandic farmers is finding out why the environmental variation is bigger than in Denmark. That will require further data gathering to get an estimation of the problem. The Bulmer effect could possibly explain the lower genetic variance.

Another area of interest is including total pedigree information recorded about individuals when moved between farms. This would result in information about genetic connectedness between “herds” and also a better estimation of the inbreeding coefficient. This is especially important for farms that import a lot of their breeding stock each year. It is difficult to know the actual state of inbreeding with the information available unless a microsatellite study is done similar to the one done by Demontis et al (2011).

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7. Table of Figures

8. List of Tables