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Genomic selection in American mink (*Neovison vison*) using a single-step genomic best linear unbiased prediction model for size and quality traits graded on live mink

Trine M. Villumsen,[†,1] Guosheng Su,[†] Bernt Guldbrandtsen,[‡] Torben Asp,[†] and Mogens S. Lund[†]

[†]Center for Quantitative Genetics and Genomics, Aarhus University, 8830 Tjele, Denmark, [‡]Animal Breeding, Department of Animal Science, University of Bonn, 53115 Bonn, Germany

[1]Corresponding author: tmv@qgg.au.dk

Abstract

Genomic selection relies on single-nucleotide polymorphisms (**SNP**s), which are often collected using medium-density SNP arrays. In mink, no such array is available; instead, genotyping by sequencing (**GBS**) can be used to generate marker information. Here, we evaluated the effect of genomic selection for mink using GBS. We compared the estimated breeding values (**EBV**s) from single-step genomic best linear unbiased prediction (**SSGBLUP**) models to the EBV from ordinary pedigree-based BLUP models. We analyzed seven size and quality traits from the live grading of brown mink. The phenotype data consisted of ~20,600 records for the seven traits from the mink born between 2013 and 2016. Genotype data included 2,103 mink born between 2010 and 2014, mostly breeding animals. In total, 28,336 SNP markers from 391 scaffolds were available for genomic prediction. The pedigree file included 29,212 mink. The predictive ability was assessed by the correlation (r) between progeny trait deviation (**PTD**) and EBV, and the regression of PTD on EBV, using 5-fold cross-validation. For each fold, one-fifth of animals born in 2014 formed the validation set. For all traits, the SSGBLUP model resulted in higher accuracies than the BLUP model. The average increase in accuracy was 15% (between 3% for fur clarity and 28% for body weight). For three traits (body weight, silky appearance of the under wool, and guard hair thickness), the difference in r between the two models was significant ($P < 0.05$). For all traits, the regression slopes of PTD on EBV from SSGBLUP models were closer to 1 than regression slopes from BLUP models, indicating SSGBLUP models resulted in less bias of EBV for selection candidates than the BLUP models. However, the regression coefficients did not differ significantly. In conclusion, the SSGBLUP model is superior to conventional BLUP model in the accurate selection of superior animals, and, thus, it would increase genetic gain in a selective breeding program. In addition, this study shows that GBS data work well in genomic prediction in mink, demonstrating the potential of GBS for genomic selection in livestock species.

Key words: genomic selection, genotyping-by-sequencing, live quality traits, *Neovison vison*

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Abbreviations

BLUP	best linear unbiased prediction
BV	breeding value
EBV	estimated breeding value
GBS	genotyping by sequencing
MAF	minor allele frequency
PTD	progeny trait deviation
SNP	single-nucleotide polymorphism
SSGBLUP	single-step genomic best linear unbiased prediction

Introduction

In the mink industry, the main objective is to produce large dried skins of high quality for sale, preferably from females with large litters. However, the breeding program for mink suffers from a number of characteristics that make it difficult for the breeder to achieve a balanced genetic progress for target traits. First, genetic evaluation of fertility traits has a low accuracy because heritabilities (h^2) for fertility traits are low (Koivula et al., 2011; Thirstrup et al., 2019). Female reproductive capacity is limited as mink are monoestrous and only have one litter per year (Mononen et al., 2012). In addition, about 60% of females only get one litter before they are pelted, and only females capable of weaning a large litter with high body weights may get a second breeding season. Males usually breed 5 to 10 females and are pelted afterward. Therefore, selection intensities are low. Second, pelt size and pelt quality records are not available for selection candidates. Instead, body weight and quality recorded for live animals are used as indicator traits for pelt size and pelt quality. Both have medium to high h^2 (Thirstrup et al., 2017, 2019). Finally, there is a negative genetic correlation between litter size and body weight (Koivula et al., 2011), so selection for body weight leads to large animals with low fertility because phenotypic selection for larger animals is much more efficient than selection for higher fertility.

In pigs, Guo et al. (2015) found that models including genomic information resulted in higher accuracies for the low heritable fertility traits than a pure pedigree-based model. The increased accuracies for models that include genomic information might be used in mink to obtain a more balanced selection. In addition, the use of indicator traits that are genetically correlated to the traits of interest in mink suggests that genomic selection may be a good solution for improving the genetic evaluation (Meuwissen et al., 2001, Calus and Veerkamp, 2011). Genomic selection has successfully been applied in many livestock species, such as cattle, pigs, and poultry (e.g., VanRaden et al., 2009; Christensen et al., 2012; Wolc et al., 2015). It makes use of genome-wide dense marker sets to predict genetic values of candidate animals (Meuwissen et al., 2001). A single-step genomic best linear unbiased prediction (**SSGBLUP**) model was proposed (Legarra et al., 2009; Christensen and Lund 2010) to use the phenotypic information of both genotyped and non-genotyped individuals for genomic prediction efficiently. The SSGBLUP combines genotypic, phenotypic, and pedigree information for estimating breeding value and thereby results in higher accuracies of the estimated breeding values (**EBV**s).

Genomic selection in livestock usually uses **SNP** (single-nucleotide polymorphisms) arrays for genotyping. However, no SNP array is currently available for mink. Alternatively, genotypes of SNP markers can be obtained in a price-efficient manner by genotyping by sequencing (**GBS**). Poland et al. (2012) presented a GBS-based approach to genomic prediction in barley and wheat, which has also been applied in genomic selection in aquaculture (Robledo et al., 2018).

The assembly of the mink genome by Cai et al. (2017) has made the genomic prediction in mink breeding feasible. The current study is (to our knowledge) the first study to examine the impact of genomic selection in mink. We did so by testing whether prediction accuracies of breeding values estimated from SSGBLUP and a conventional pedigree-based best linear unbiased prediction (**BLUP**) approaches were significantly different.

Materials and Methods

Animals and phenotypic data

A total of 20,639 Brown mink (*Neovison vison*) born during the period from 2013 to 2016 in Foulum Research Farm, Aarhus University, Denmark, were used in this study. The mink were housed and later pelted in accordance to the Danish legislation for mink production (Danish Ministry of Environment and Food, 2015), tissue samples were collected postmortem, and, therefore, no ethical approval was needed for this study.

In their first year, the mink were graded by professional fur quality evaluators from Kopenhagen Fur after maturation of the winter fur in November. Mink were graded for fur quality: 1 to 5 (5 being best), under wool density: 1 to 3 (flat-filling), silky appearance: 1 to 3 (normal-silky), fur clarity: 1 to 3 (red-blue), guard hair thickness: 1 to 3 (thick-thin), and guard hair length: 1 to 5 (long-short). Body weight was also measured at the live grading in November. A more detailed explanation of the traits can be found in Thirstrup et al. (2017). The pedigree file was extracted from the Fur Farm database held by the Danish fur breeders association. The pedigree encompassed 29,212 brown mink.

Genotypes

Tissue for DNA extraction was collected from the muscle Mm. interossei in a toe after culling of the mink. We extracted genomic DNA from 2,103 brown mink born from 2010 to 2014 at Foulum Research Farm, Aarhus University, Denmark. The genotyped mink were primarily breeding animals and their progeny. As a consequence, more females than males were genotyped. Table 1 summarizes the distribution of the 2,103 genotyped mink in relation to year of birth and sex.

The mink were genotyped by GBS method (Elshire et al., 2011), reads were aligned using Burrows-Wheeler Alignment tool (Li and Durbin, 2009), variant calling was done using GATK's HaplotypeCaller (Poplin et al., 2018, preprint), and GATK's SelectVariants and VariantAnnotator was used to filter for biallelic sites and to annotate for Allele Balance, respectively. In the GBS protocol, the genome was cut with PstI (cut site: CTGCAG) and MspI (cut site: CCGG). There were 2,081,313 SNPs

Table 1. The number of genotyped males and females born from 2010 to 2014

Birth year	Males	Females	Total
2010	1	97	98
2011	3	226	229
2012	6	439	445
2013	187	391	578
2014	193	560	753
Total	390	1,718	2,103

with a mean depth per site of 10.08 before filtering. We obtained a filtered set of variants using vcftools (https://github.com/vcftools/vcftools) with the parameters mac 3, minQ 30, max-missing 0.5, minDP 3, maf 0.01, max-meanDP 102, and hwe 1e-05 followed by vcffilter, which is a part of vcflib (https://github.com/vcflib/vcflib) using the command *vcffilter -s -f "ABHet > 0.35 & ABHet < 0.65 & ABHom > 0.85" in.vcf > out.vcf*. After filtering, we obtained a total of 28,336 SNP, mapping to 391 scaffolds (mean: 72.5 SD: 123.6) with minor allele frequency (**MAF**) > 0.02, at least 80% calls per individual (Cai et al., 2018) and an average of 97% individuals called for each marker.

Statistical models

Breeding values were estimated using a conventional pedigree-based BLUP method and an SSGBLUP method. The difference between the two methods is the information used to construct the relationship matrices.

Variance components and breeding values were estimated using BLUP and SSGBLUP. We used a single-trait model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wp} + \mathbf{Za} + \mathbf{e} \quad (1)$$

where $\mathbf{y}$ is the vector of phenotype, $\boldsymbol{X}$ is the design matrix for fixed effects, $\boldsymbol{b}$ is the vector of fixed effects, $\boldsymbol{W}$ is the design matrix that relates common litter effect to phenotypes, $\boldsymbol{p}$ is a vector of common litter effect, $\boldsymbol{Z}$ is the design matrix that relates animals to phenotype, $\boldsymbol{a}$ is the vector of animal additive genetic effects, and $\boldsymbol{e}$ is the vector of random residual effects. It was assumed that $\boldsymbol{p} \sim N(\mathbf{0}, I\sigma_c^2)$ where I is an identity matrix, σ_c^2 is the variance of litter effects, $\boldsymbol{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ when using BLUP or $\boldsymbol{a} \sim N(\mathbf{0}, \boldsymbol{H}\sigma_a^2)$ when using SSGBLUP, where $\mathbf{A}$ is the pedigree-based relationship between individuals, and $\boldsymbol{H}$ is the genotype and pedigree joint relationship matrix (see details below), σ_a^2 is the additive genetic variance, $\boldsymbol{e} \sim N(\mathbf{0}, I\sigma_e^2)$, where I is an identity matrix and σ_e^2 is the residual variance.

The fixed effects in the models were sex, birth year, and shed within the year. The random effects were common litter and additive genetic effects.

The joint relationship matrix $\boldsymbol{H}$ was constructed by combining the pedigree relationship matrix $\mathbf{A}$ and the genomic relationship matrix $\boldsymbol{G}$ (Legarra et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010). The genomic relationship matrix $\boldsymbol{G}$ was constructed according to VanRaden (2008), that is, $\mathbf{G} = \frac{\mathbf{ZZ}'}{2\Sigma\ p_j(1-p_j)}$, where p_j is the frequency of the second allele for the jth SNP, and the elements in the matrix $\mathbf{Z}$ is 0-2p_j for homozygous 11, 1-2p_j for heterozygous 12 and 21, and 2-2p_j for homozygous 22. The combined relationship matrix $\boldsymbol{H}$ was constructed as:

$$\boldsymbol{H} = \begin{bmatrix} \boldsymbol{G}_w & \boldsymbol{G}_w\mathbf{A}_{11}^{-1}\mathbf{A}_{12} \\ \mathbf{A}_{21}\mathbf{A}_{11}^{-1}\boldsymbol{G}_w & \mathbf{A}_{21}\mathbf{A}_{11}^{-1}\boldsymbol{G}_w\mathbf{A}_{11}^{-1}\mathbf{A}_{12} + \mathbf{A}_{22} - \mathbf{A}_{21}\mathbf{A}_{11}^{-1}\mathbf{A}_{12} \end{bmatrix} \quad (2)$$

Where $\mathbf{A}_{11}$ is the submatrix of $\mathbf{A}$ for the genotyped mink, $\mathbf{A}_{22}$ is the submatrix of $\mathbf{A}$ for the non-genotyped mink, $\mathbf{A}_{12}$ and $\mathbf{A}_{21}$ are the submatrices of $\mathbf{A}$ between genotyped and non-genotyped mink, respectively, and $\boldsymbol{G}_w$ is the improved genomic relationship, $\boldsymbol{G}_w = w\boldsymbol{G} + (1-w)\mathbf{A}_{11}$, where w is the fraction of genetic variance not captured by the markers (Christensen et al., 2012). In this study, w = 0.30 was chosen according to some previous studies in pig (Christensen et al., 2012; Guo et al., 2015; Xiang et al., 2016). The inverse of $\boldsymbol{H}$ was:

$$\boldsymbol{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \boldsymbol{G}_w^{-1} - \mathbf{A}_{11}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} \quad (3)$$

We used the same variance components for both conventional and genomic predictions. The variance components for the base population were estimated from all available phenotypic data from 2013 to 2016 using the linear model (1) with pedigree-based/combined relationship matrix by restricted maximum likelihood in the software DMU (Madsen et al., 2014). Breeding values were also estimated in the DMU package. The phenotypic records of body weight were standardized to a mean of 0, and a variance of 1 within sex, due to the sex-specific differences in body weight in mink, where males are twice as heavy as females.

Table 2 summarizes the number of phenotypic records for the estimation of variance components, progeny trait deviation (**PTD**) and EBVs, respectively, and the mean and SD of each trait prior to the standardization of body weight to mean 0 and variance 1.

Validation

The predictive ability of the traditional BLUP and genomic SSGBLUP model was assessed using 5-fold cross-validation. In each of 5-fold, one-fifth of animals born in 2014, the last year with genotyped animals, were assigned to the validation set, and their phenotypic records were discarded. The remaining four-fifth of animals born in 2014 and all the animals born in 2013 formed the reference set. The split into the five validation sets was based on paternal half-sib families, such that all individuals of each paternal half-sib and full-sib family

Table 2. The number of phenotypic records and mean in the datasets used for estimation of variance components, PTD, and EBV, respectively (SD given in brackets)

Trait	Records up to 2016 Estimation of variance components		Records up to 2015 Estimation of PTD		Records up to 2014 Estimation of EBV	
	N	Mean	N	Mean	N	Mean
Body weight, g	10,043[m1]	3,872 (552)	7,635[m]	3,818 (546)	5,002[m]	3,739 (524)
	10,241[f1]	2,028 (314)	7,688[f]	1,987 (305)	4,824[f]	1,953 (96)
Density	20,574	2.23 (0.43)	15,259	2.22 (0.43)	9,776	2.21 (0.42)
Quality	20,574	3.45 (0.76)	15,259	3.42 (0.79)	9,776	3.42 (0.82)
Silky	20,571	2.06 (0.57)	15,258	2.01 (0.58)	9,775	1.96 (0.61)
Guard hair thickness	20,563	2.03 (0.64)	15,253	2.02 (0.62)	9,775	2.01 (0.60)
Guard hair length	20,573	2.93 (0.66)	15,258	2.86 (0.65)	9,775	2.88 (0.64)
Fur clarity	20,573	2.13 (0,77)	15,258	2.10 (0.80)	9,775	2.06 (0.80)

[1,m] and [f]refer to male and female records, respectively.

Table 3. For each validation fold for 2014 records, this shows the number of phenotypic records discarded, total, and from genotyped validation animals with progeny, the number of litters, and number of sires for the litters

	Discarded records			Hereof from validation animals with PTD		
Validation fold	*N*	Litters	Sires	*N*	Litters	Sires
1	1,080	192	61	100	53	26
2	1,042	194	62	90	56	30
3	1,039	193	63	78	43	24
4	1,059	205	68	85	46	24
5	981	174	50	141	75	31
Total	5,201	958	304	494	273	135

were assigned to the same validation set. The EBVs from the validation animals in each fold were joined such that the set of animals born in 2014 formed the combined validation set, in which accuracies and regressions were computed. In total, we had phenotypic records from about 9,800 mink born in 2013 and 2014 for each trait. These records were used for the estimation of breeding values. Of the 9,800 mink, 1,331 were genotyped. About 1,000 phenotypic records were discarded in each validation fold (981 to 1,080), hereof about 100 from genotyped mink with progeny in each fold (78 to 141). Table 3 specifies the number of discarded phenotypic records in each validation fold, and how many of these are from genotyped individuals with progeny. Table 3 also specifies the number of litters and sires of the litters in each fold.

The predictive ability of the two models was assessed by the accuracy of the EBV from the BLUP and the SSGBLUP models for genotyped validation animals that had progeny in 2015. The PTD was defined as the average of the progeny's performance adjusted for fixed and nongenetic random effects of the progeny as well as the genetic effect of mates. The PTDs were estimated using a conventional single-trait animal model BLUP in the DMU package (Madsen et al., 2014). Phenotypic records until 2015 were included, because these were needed for the estimation of PTD to the validation animals born in 2014.

The correlation between PTD and EBV (Cor(PTD, EBV)) was calculated as a weighted correlation using a weighting factor w_{PTD}, to account for heterogeneous residual variance of PTD due to different amount of information for PTD:

$$w_{PTD} = \frac{r^2_{PTD}}{(1 - r^2_{PTD})} \quad (4)$$

where r^2_{PTD} is the model reliability of PTD, which depends on the number of progeny contributing to the PTD (*nPTD*), and the h^2.

$$r^2_{PTD} = \frac{nPTD}{nPTD + (\frac{4-h^2}{h^2})} \quad (5)$$

Table 4 summarizes the average r^2_{PTD} and w_{PTD} for the genotyped validation animals with progeny.

The validation accuracy is:

$$r_{EBV} = cor(PTD, EBV)/\sqrt{r^2_{PTD}} \quad (6)$$

The cov.wt function in the R package (version 3.4.4) was used to estimate a weighted correlation. We estimated the 95% confidence interval for the difference between the validation accuracies from the SSGBLUP and BLUP model ($r_{EBV,SSGBLUP}$-$r_{EBV,BLUP}$) using nonparametric bootstrap based on 10,000 bootstrap samples. In addition, we used a *t*-test *to test the hypothesis that the difference between correlations was 0*.

Table 4. Average PTD reliability, r^2_{PTD}, and weighting factor, w_{PTD}, for the genotyped validation animals with progeny (SD given in brackets)

Trait	r^2_{PTD}	w_{PTD}
Body weight	0.50 (0.20)	1.54 (1.58)
Quality	0.40 (0.19)	0.96 (0.99)
Density	0.17 (0.13)	0.24 (0.25)
Silky	0.34 (0.19)	0.72 (0.74)
Guard hair length	0,46 (0.20)	1.28 (1.31)
Guard hair thickness	0.40 (0.19)	0.97 (1.00)
Fur clarity	0.29 (0.17)	0.54 (0.55)

The bias of EBVs from the two models was assessed from the regression coefficients of EBVs from the full data including all records up to 2014 on EBV for validation animals with genotypes and progenies in the five validations. The expectation was 1, if there was neither over nor under dispersion (Legarra and Reverter, 2018).

Results

We estimated variance components using single-trait animal models with both BLUP and SSGBLUP methods based on full data (Table 5). The estimates of σ^2_c, σ^2_c, and σ^2_e were not significantly different for the two models based on *t*-tests. *Most* of the traits had low to medium h^2 varying from 0.092 for density in the BLUP model to 0.530 for body weight in the SSGBLUP model.

The accuracies of the prediction of EBV from the two models and the increase from BLUP-EBV to SSGBLUP-EBV are presented in Table 6. For all traits, the SSGBLUP model resulted in higher accuracies than the BLUP model. The accuracies ranged from 0.298 for fur clarity in the BLUP model vs. 0.308 in the SSGBLUP model to 0.673 for silky appearance of the under wool in the BLUP model to 0.753 in the SSGBLUP model. The increases ranged from 3% for fur clarity to 28% for body weight, and the average increase in accuracy was 15%. Table 6 also presents the confidence interval for the difference between the correlations from the two models, estimated using 10,000 bootstrap samples. For body weight, silky appearance of the under wool, and guard hair thickness, there were significant increases in accuracy with the SSGBLUP model, and, in addition, the 95% confidence intervals did not include 0, indicating that the SSGBLUP model resulted in significantly higher prediction accuracy than the BLUP model for these traits.

Bias in the genetic evaluations was measured by the regression of genetic evaluations on PTD for validation animals

Table 5. Genetic variance (σ^2_a), common litter variance (σ^2_c), residual variance (σ^2_e), and heritability (h^2) of body weight and quality traits estimated by BLUP and SSGBLUP using all data records until 2016 (SE given in brackets)

Trait	BLUP				SSGBLUP			
	σ^2_a	σ^2_c	σ^2_e	h^2	σ^2_a	σ^2_c	σ^2_e	h^2
Body weight[1]	0.414	0.077	0.299	0.524	0.419	0.077	0.295	0.530
	(0.021)	(0.005)	(0.011)		(0.021)	(0.005)	(0.011)	
Quality	0.183	0.025	0.324	0.345	0.187	0.023	0.321	0.352
	(0.012)	(0.003)	(0.007)		(0.012)	(0.003)	(0.007)	
Density	0.016	0.006	0.155	0.092	0.018	0.005	0.155	0.099
	(0.002)	(0.001)	(0.002)		(0.002)	(0.001)	(0.002)	
Silky	0.079	0.016	0.204	0.263	0.078	0.015	0.203	0.264
	(0.006)	(0.002)	(0.004)		(0.005)	(0.002)	(0.004)	
Guard hair length	0.187	0.016	0.208	0.456	0.189	0.015	0.207	0.460
	(0.010)	(0.002)	(0.006)		(0.010)	(0.002)	(0.006)	
Guard hair thickness	0.138	0.018	0.240	0.349	0.138	0.017	0.239	0.349
	(0.009)	(0.002)	(0.005)		0.009)	(0.002)	(0.005)	
Fur clarity	0.116	0.028	0.439	0.200	0.116	0.028	0.438	0.200
	(0.010)	(0.004)	(0.007)		(0.010)	(0.004)	(0.007)	

[1] Original records within sex were standardized to mean = 0, variance = 1, and the records of males and females were analyzed together.

Table 6. Accuracy of BLUP-BV and SSGBLUP-BV for the genotyped validation animals with progeny, the increase in accuracy of EBV from the SSGBLUP model relatively to the BLUP model, and 95% confidence interval for the difference of cor(PTD,EBV) from the two models based on 10,000 bootstrap samples (SE given in brackets)

Trait	Accuracy BLUP-BV	Accuracy SSGBLUP-BV	Increase in accuracy, %	95% confidence interval
Body weight	0.38 (0.07)	0.49 (0.07)	28*	0.019 to 0.159
Quality	0.53 (0.08)	0.59 (0.08)	10	–0.005 to 0.092
Density	0.37 (0.16)	0.44 (0.15)	18	–0.005 to 0.086
Silky	0.67 (0.08)	0.75 (0.08)	12*	0.014 to 0.099
Guard hair length	0.47 (0.09)	0.52 (0.08)	12	–0.011 to 0.105
Guard hair thickness	0.55 0.08)	0.65 (0.07)	19*	0.036 to 0.119
Fur clarity	0.30 (0.11)	0.31 (0.11)	3	–0.043 to 0.058
Average	0.47	0.53	15	—

*Significant increase based on *t*-test, $P < 0.05$.

with genotypes and progenies in the five validations. The regressions are presented in Table 7. Both negative and positive biases were observed for EBV from both BLUP and SSGBLUP models. For three traits, a *t*-test *implied that regression coefficients were different from 1. The lowest regression coefficient was observed for density (0.790 and 0.856 for BLUP and SSGBLUP, respectively). The highest* was observed for silky appearance of the under wool (1.600 and 1.469 for BLUP and SSGBLUP model, respectively). Another trait with regression coefficients deviating from 1 was quality. Inclusion of genomic information in the relationship matrix tended to reduce the over or under dispersion of EBVs with regression coefficients deviating less from 1 for five out of seven traits. However, there was no significant difference in the regression coefficients for the two models for any trait.

Discussion

This study is the first to investigate the benefit of genomic prediction in a real mink population. We compared genetic evaluation using the SSGBLUP model with conventional pedigree-based BLUP model. We found that it was possible to perform a genetic evaluation based on GBS data with a relatively small number of genotyped mink. A comparison of the EBV from the models indicated that the SSGBLUP model led to higher accuracy and less bias of EBV than the pedigree-based BLUP model. Fur clarity did not increase in accuracy with an SSGBLUP model. This could be because the models we used for the analyses assumed normally distributed traits. This seemed reasonable for most of the traits based on data distributions; although, most of the traits only had few categories. However, for fur clarity, the observations were almost uniformly distributed; therefore, the prediction model might have failed. We have tried to estimate EBV for all traits with categorical liability threshold models, but the analyses did not converge, and the data set might be too small for these analyses. A larger data set might allow the use of a categorical model, especially for fur clarity.

In many livestock species, genomic selection uses commercial SNP arrays for genotyping, for example, the BovineSNP50k BeadChip for cattle, the PorcineSNP60k BeadChip for pig, and the 60k BeadChip for chicken, all from Illumina Inc, San Diego, CA. As there was no SNP chip for mink, the technique GBS was used for genotyping of the mink. Many simulation studies have suggested using GBS in livestock populations (Gorjanc et al., 2015; Wang et al., 2019); however, until now, the technique is mostly used in plant breeding. The results from this study confirmed that GBS is a viable alternative to using an SNP chip for genomic prediction.

In this study, the number of genotyped animals was relatively small. However, the accuracies for EBV estimated in BLUP and SSGBLUP models confirmed that the inclusion of

Table 7. Bias in the dispersion of BLUP and SSGBLUP EBVs measured as the regressions of EBVs from full data with records up to 2014 on EBV from five validation folds, for genotyped validation animals with progeny (SE given in brackets)

Trait	BLUP	SSGBLUP
Body weight	1.121 (0.071)	1.089 (0.054)
Quality	1.264 (0.061)[1]	1.198 (0.045)[1]
Density	0.790 (0.038)[1]	0.856 (0.035)[1]
Silky	1.600 (0.072)[1]	1.469 (0.053)[1]
Guard hair length	1.006 (0.058)	1.022 (0.048)
Guard hair thickness	0.991 (0.046)	1.039 (0.037)
Fur clarity	0.951 (0.076)	1.029 (0.059)

[1]Significantly different from 1, $P < 0.05$.

marker information in a single-step approach produced more accurate EBV estimates for the genotyped animals. The average increase in accuracy for the seven traits was 14.6% when EBV was estimated using the SSGBLUP model, even with the relatively small number of genotyped animals. This increased accuracy indicates that the SSGBLUP model results in a more correct ranking of individuals and thereby a higher potential for maximizing genetic progress. This increase could be caused by the information about the Mendelian sampling term in the SSGBLUP model. The extra gain from genomic information was confirmed by bootstrapping statistics and a significant increase in accuracy. Many previous studies in livestock species also concluded that SSGBLUP evaluations provided more accurate EBV estimates than the traditional BLUP model based on pedigree. Christensen et al. (2012) found that correlations between BLUP-BV, SSGBLUP-BV, and corrected phenotypes increased from 0.179 to 0.353 for daily gain in genotyped pigs and from 0.196 to 0.231 for feed conversion ratio. Su et al. (2012) reported that reliability increased from 0.199 using BLUP to 0.322 using SSGBLUP, averaged over 15 traits in the Red cattle population. Gao et al. (2018) found reliabilities increased by 55% to 85% for milk, fat, and protein for genotyped cows going from a pedigree-based BLUP to SSGBLUP model. Yoshida et al. (2019) studied a population of rainbow trout and found an increase in reliability going from pedigree-based BLUP to SSGBLUP of 7% to 11% for survival traits. These studies and many others all used SNP chip for genotyping.

The h^2 estimates for all traits were similar for the two models. The medium to high h^2 estimates indicated that all traits could be genetically improved by selection. The estimates of the h^2 were in concordance or higher than previous estimates for body size and live quality traits in Danish mink reported by Thirstrup et al. (2017). However, different studies, in general, have shown large discrepancies in h^2 estimates for body size and quality traits in mink, depending on the population and the trait definition. For examples, Koivula et al. (2011) found a h^2 of 0.19 for body size in Finnish mink, and Kołodziejczyk and Socha (2012) estimated a h^2 of 0.11 for body weight in American mink.

The regression coefficient of EBVs from all records up to 2014 on EBVs from the five validation folds for the genotyped validation animals with progeny is a measure of dispersion of predictions (Legarra and Reverter, 2018). A regression slope of 1 indicates no positive or negative bias. In this study, four out of the seven regression coefficients were not significantly different from 1 for both models. However, for all traits, the regression slopes for SSGBLUP-BV were closer to 1, indicating that SSGBLUP models resulted in less bias of the EBV than the BLUP model.

Conclusions

This study supports the potential of GBS for genomic selection in livestock species. The single-step method provided more accurate estimates of EBV for the genotyped mink than the pedigree-based BLUP model. Bootstrap confidence interval and hypothesis test supported the statistical significance of the superiority of the SSGBLUP model to the BLUP model. Regression coefficients of EBVs based on all records up to 2014 on EBVs from the five validation folds for the genotyped validation animals with progeny were closer to 1 for the SSGBLUP-BV, indicating less bias of the EBVs from SSGBLUP than those from the BLUP model.

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Conflicts of interest statement

The authors declare that they have no conflicts of interest.

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