Heritability of litter size in the Swedish population of Shetland sheepdogs

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Abstract

The Shetland sheepdog is one of the most common canine breeds in Sweden and the demand for puppies is arguably high on the Swedish market. However, the continuously small litter sizes (mean of 3.0-3.4) in the population have been a cause for concern. Previous studies have presented low to medium heritability estimates of litter size in other dog breed populations, but there is no such estimate for the Shetland sheepdog. In this retrospective study, data from 10 443 Shetland sheepdog litters born and registered in the Swedish kennel club between 1980 and 2021 was used to estimate litter size heritability and analyse environmental variables affecting the trait. The study showed that dam age and parity had significant effects on litter size. Sire inbreeding had a significant positive effect (+2.7, SE=1.2) when also adjusting for the inbreeding coefficients of the litter and dam. Litter inbreeding had a significant negative effect (-1.6, SE=0.6) on litter size when included separately in the model, while no significant effect of dam inbreeding was found. The heritability of litter size was estimated between 0.14 (SE=0.02) and 0.22 (SE=0.05), with the most reliable estimate being 0.15 (SE=0.02). The results indicate that a breeding progress to increase litter sizes in the Swedish Shetland sheepdog population is possible with the implementation of best linear unbiased prediction (BLUP) based breeding values, if the trait is prioritised when selecting breeding animals.

Keywords: dog, breeding, litter size, inbreeding, heritability, Shetland sheepdog

Sammanfattning

Shetland sheepdog är en av de vanligast förekommande hundraserna i Sverige och efterfrågan på valpar kan anses stor. Populationen har dock haft kontinuerligt små kullar med en årlig medelkullstorlek på 3,0–3,4 valpar. Tidigare studier har presenterad låga till medelhöga arvbarhetsskattningar för kullstorlek i andra hundraspopulationer, men inga tidigare skattningar har gjorts av arvbarheten för kullstorlek hos Shetland sheepdog. I denna retrospektiva studie användes data från 10 443 kullar av rasen Shetland sheepdog, födda och registrerade i Svenska Kennelklubben mellan åren 1980 och 2021. Arvbarheten för kullstorlek skattades och olika miljöfaktorers påverkan på egenskapen analyserades. Studien visade att moderns ålder och kullnummer hade signifikant effekt på kullstorleken. Faderns inavelskoefficient hade en signifikant positiv påverkan (+2,7, SE=1,2) på kullstorleken, men bara när även inavelskoefficienter för moder och kull var inkluderade i den statistiska modellen. Kullens inavelskoefficient hade en signifikant negativ effekt (-1,6, SE=0,6) på kullstorleken när inga andra inavelskoefficienter justerades för i modellen. Arvbarheten för kullstorlek skattades mellan 0,14 (SE=0,02) och 0,22 (SE=0,05), där en skattning på 0,15 (SE=0,02) ansågs som mest tillförlitlig. Resultatet av denna studie indikerar att det går att nå ett avelsframsteg för ökade kullstorlekar i populationen med hjälp av *best linear unbiased prediction* (BLUP) baserade avelsvärden. Detta förutser dock att egenskapen kullstorlek prioriteras vid selektion av avelsdjur.

Nyckelord: hund, avel, kullstorlek, inavel, arvbarhet, Shetland sheepdog

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Abbreviations

BLUP	Best Linear Unbiased Prediction
F	Inbreeding coefficient
h^2	Estimated heritability
SKK	Svenska Kennelklubben, The Swedish kennel club

1. Introduction

The Shetland sheepdog has long been one of the most popular dog breeds in Sweden. In 2020 it was the sixth most common breed, in terms of number of yearly registered individuals in the Swedish kennel club (Svenska Kennelklubben, SKK), with 1 071 new registrations (SKK 2021b). In Sweden it is mandatory by law to permanently mark and register all dogs before the age of 4 months in a central dog register governed by the Swedish Board of Agriculture (Jordbruksverket 2022a). Dog owners must also register when their dogs die. On the 31st of December 2021, a total of 10 826 Shetland sheepdogs were registered in Sweden (Jordbruksverket 2022b).

Several canine multi-breed studies have shown that breed and body size is significantly related to litter size, where breeds with larger body size have larger litters (Kania-Gierdziewicz & Pałka 2019; Leroy et al. 2015; Borge et al. 2011). The Swedish population of Shetland sheepdogs have had continuously small mean litter sizes (previously measured to a mean of about 3.2 registered puppies per litter) compared to Swedish populations of breeds of similar body size, such as the Cairn terrier (4.1), Cavalier king Charles spaniel (3.8), Bichon Frisé (4.0) and Pug (3.5) (SSSK 2019). There is arguably a high demand for Shetland sheepdog puppies on the Swedish market, making a more prolific reproduction desirable. In the Shetland sheepdog breed-specific breeding strategy, the breed club shows an interest in gathering more knowledge about breed fertility, with an ultimate goal of being able to present breeding strategies aiming to increase litter sizes (SSSK 2019).

1.1 Previous studies

The definition of dog litter size varies between previous studies. Litter size has previously been defined as the total number of puppies born (alive and dead) (Borge et al. 2011), number of puppies alive at whelping (Andrade et al. 2021; Chu et al. 2019; Mandigers et al. 1994) or number of puppies alive at registration in the local kennel club (Kania-Gierdziewicz & Pałka 2019; Leroy et al. 2015; Borge et al. 2011; Urfer 2009). Several studies have furthermore considered different definitions of litter size for the same population. Šichtař et al. (2016) defined litter size in a population of German shepherd dogs as the total number of puppies born, dead and alive, but did also consider the trait defined as number of puppies born alive. Gavrilovic et al. (2008) considered litter sizes of the Swedish population of the Drever breed defined as number of puppies per litter registered in SKK. The authors also studied data from litters bred by one private, professional breeder, where puppies born dead or being euthanized before the age of registration were included. Schrack et al. (2017) studied litter size in a population of the Entlebucher Mountain dog, considering both total number of puppies born (dead and alive) in a litter and number of puppies per litter at registration in the Swiss national kennel club. A study by Hare & Leighton (2006) used four measurements of litter size from each litter studied in a Labrador retriever and a German shepherd dog population, namely the number of puppies born (alive and dead) and the number of puppies alive at birth, at 14 days and at 49 days. Mostert et al. (2015) defined litter size in a population of Boxers as number of puppies born and as number of puppies alive at the age of 14 days.

When defining litter size as number of puppies alive at registration potential data related to early puppy survival and fertility, such as prevalence of dystocia, may be lost. Dystocia is a broad term for disturbances that happen during labour. These disturbances may be caused by the foetus (e.g. when it is wrongly positioned, too big or if it is dead), the dam (e.g. because of physical conformation), or by a combination of both foetus and dam (Münnich & Küchenmeister 2009). Dams of small and miniature breeds have a higher risk of dystocia compared to dams of larger breeds (Münnich & Küchenmeister 2009). Number of puppies per litter have also been associated with dystocia, where the risk has been shown to increase when litter sizes are smaller and larger than expected (Cornelius et al. 2019). That study did however only include five breeds of larger size, where a small litter size was defined as five puppies or less, which is not entirely comparable to the population considered in the present study. The result of a study on 530 cases of dystocia, which included dams of 54 different breeds, did however indicate that one-puppy litters are a risk factor for dystocia across breeds of different sizes (Münnich & Küchenmeister 2009).

1.1.1 Factors affecting litter size

Litter size is a multifactorial trait, influenced by genetic and environmental factors. Previous studies have investigated the impact of various factors on dog litter size with varying results.

Year and month of birth

Birth year had a significant effect on litter size in the Dutch Kooiker dog (Mandigers et al. 1994) but not in the Entlebucher Mountain dog, German shepherd dog, Labrador retriever, Golden retriever, Beagle or the Tatra Shepherd dog (Kania-Gierdziewicz & Pałka 2019; Schrack et al. 2017; Hare & Leighton 2006).

Birth month had a significant effect on litter size in a population of German shepherd dogs where mean litter size varied greatly between months, with the largest litters at birth and registration being born in November and the smallest litters in April (Šichtař et al. 2016). Gavrilovic et al. (2008) studied reproductive patterns in the Swedish population of the Drever breed. Analyses were based on SKK data from 2717 registered litters, with additional fertility data for 224 of those litters distributed by a private SKK-affiliated kennel. Litter sizes in the private kennel differed significantly between birth seasons, with most puppies per litter being born and registered in spring, but no significant difference was found in the bigger dataset (Gavrilovic et al. 2008). Urfer (2009) found no significant influence of birth season on litter size in Irish Wolfhounds, nor did Schrack et al. (2017) in Entlebucher Mountain dogs. In addition, Borge et al. (2011) found no significant effect of birth season on litter size in 224 dog breeds, when adjusting for breed, dam age and body size in the statistical model.

Dam age and parity

Increased dam age have been shown to have a significantly negative effect on litter size in the Entlebucher Mountain dog (Schrack et al. 2017), the Dutch Kooiker dog (Mandigers et al. 1994) and the Drever dog (Gavrilovic et al. 2008). However, litter size was neither significantly affected by dam age in a population of German shepherd dogs (Šichtař et al. 2016) nor in a population of Irish Wolfhounds (Urfer 2009).

Beyond looking at the effect of dam age, the effect of the number of litters that dams have given birth to (parity) has been investigated in several studies. Parity of the dam had a significant effect on litter size in a population of German shepherd dogs (Šichtař et al. 2016) and in a population of Drever dogs (Gavrilovic et al. 2008). Parity also had a significant negative effect on litter size at registration in a population of Entlebucher Mountain dog, but was not significant when litter size was defined as number of puppies alive at whelping (Schrack et al. 2017). In a population of Irish Wolfhounds parity did not have a significant effect on litter size when included in a generalized linear model, but had a significant negative effect when analysed separately (Urfer 2009). The model used in that study did however have a low coefficient of determination (R^2=0.0341) (Urfer 2009) and the study results should therefore be considered with caution. In the German Shepherd dog, litter sizes have been observed to be largest when born in parity 2 to 5 (Šichtař et al. 2016). In another study, mean litter sizes increased until parity 2 in four breed populations and until parity 3 in the rest of the populations studied (n=3) and decreased in the following parity numbers (Leroy et al. 2015).

Inbreeding

Inbreeding is synonymous with the increase of homozygosity in a population and thereby the reduction in genetic diversity and the loss of alleles (Marelli et al. 2020; Urfer 2009). Inbreeding depression describes the negative correlation between the mean phenotypic value of a trait and an increasing level of inbreeding in a population (Marelli et al. 2020).

The effect of inbreeding on litter size have been studied in several dog populations using inbreeding coefficients (F). Inbreeding coefficients represents the probability of two alleles at a given neutral locus in a diploid individual being identical by decent (Hedrick & Garcia-Dorado 2016). The methods used when calculating F have varied in previous studies. In a study by Leroy et al. (2015) F was calculated using the PEDIG software in seven dog populations. Inbreeding was included in the linear mixed model divided into three classes (<6.25%, 6.25-12.5%, >12.5%). When level of litter inbreeding increased there was a significant decrease in litter sizes in all seven breed populations studied (Leroy et al. 2015). The same was seen for dam inbreeding in five of the seven breeds studied, whereas the level of sire inbreeding only had the same effect in two of the breeds.

In a study on Irish Wolfhounds, inbreeding of the litter, dam and sire was defined as F calculated over 5, 10, 20 and 30 generations, as well as over the whole pedigree (Urfer 2009). A linear model was used to investigate the effect of linear regressions of parental and litter inbreeding on litter size adjusting for the fixed effects of birth year, season, dam age, parity and sire age. A highly significant effect of maternal inbreeding on litter size was found when using F over 30 generations and over the whole pedigree, but neither litter nor sire inbreeding influenced litter size significantly (Urfer 2009).

Kania-Gierdziewicz & Pałka (2019) investigated the effect of inbreeding in five dog breed populations using a linear model including the linear regression coefficient of dam and sire inbreeding and the fixed effect of breed and birth year (Kania-Gierdziewicz & Pałka 2019). Litter inbreeding was also adjusted for in a separate model, including the fixed effects of breed and birth year. The study showed that neither the inbreeding level of the dam nor of the sire was significantly correlated (Spearman correlation) to litter size in any of the five breeds studied. Also litter inbreeding did not affect litter size significantly in any of the breeds (Kania-Gierdziewicz & Pałka 2019). Similar results were obtained in a study on Dutch Kooiker dogs, where litter inbreeding was negatively related and sire inbreeding positively related to litters size, however nonsignificant (Mandigers et al. 1994).

In contrast, dam inbreeding and sire inbreeding had both significant negative effects on litter size at birth in the Entlebucher Mountain dog, but only dam inbreeding had the same effect on litter size at registration (Schrack et al. 2017). Litter inbreeding had a positive nonsignificant correlation to birth year, where an increase in litter inbreeding over time was associated with a decrease in litter size, both at registration and at birth (Schrack et al. 2017).

Chu et al. (2019) found a significant negative correlation between dam inbreeding and litter size when coefficients of inbreeding were based on genomic measures (runs of homozygosity) in 93 Golden retrievers. With a 10 percent increase in dam inbreeding coefficient, a reduction of almost one puppy per litter was expected in that population. Andrade et al. (2021) based inbreeding coefficients on three generations for dams and sires and on four generations for litters in a study on litter size in a population of German spitz dogs. All sires included in that study had an F of 0, and sire inbreeding had consequently no effect on litter size. Although most dams and litters had an F of 0 (83% and 75% respectively), both dam and litter inbreeding had significant negative effects on litter size (Andrade et al. 2021).

1.1.2 Heritability

Hare & Leighton (2006) estimated litter size heritability in two populations of Labrador retrievers and German shepherd dogs in a service dog breeding colony. A linear model was used to investigate environmental contributors to litter size variation, including the factors of contemporary group, birth year, birth season and parity as fixed effects. Because of the standardised settings at the breeding colony, the authors had access to four measures of litter size from litters born between 1971 and 2004. The estimated litter size heritability was 0.24 (number of puppies born, alive and dead), 0.28 (number of puppies alive at birth), 0.28 (number of puppies alive at 14 days) and 0.31 (number of puppies alive at 49 days) in the Labrador retriever population, based on data from 618 litters. In the German shepherd dog population, the corresponding heritability was estimated to 0.19, 0.21, 0.25 and 0.26 respectively, based on data from 703 litters. The results indicated that it would be possible to select for bigger litters in both populations (Hare & Leighton 2006).

A study by Leroy et al. (2015) estimated the heritability of litter size, defined as number of puppies alive at registration in the French Kennel Club, in seven dog breed populations. The breeds studied were the Bernese Mountain dog, Basset hound, Cairn terrier, Epagneul Breton, German shepherd dog, Leonberger and West highland white terrier and data was derived from litters born between 1990 and 2012. A repeatability animal model, where litter size was considered a trait of the dam, was used, including parity and birth year as fixed effects, the random effect of breeder, the permanent random effect of the dam across all her litters and the random genetic effect of the dam (Leroy et al. 2015). Inbreeding coefficients of litter, dam and sire was also adjusted for in the model. The heritability estimate was lowest (0.06) in the Basset hound population where 3468 litter observations were included, and highest (0.11) in the Bernese Mountain dog population where 7566 litter observations were included. The authors concluded that a selection based on phenotype could possibly be used to increase litter sizes in the studied populations, but not until the quality as well as number of observations have been improved (Leroy et al. 2015).

A study by Mostert et al. (2015) estimated heritability of litter size at birth (dead and alive puppies per litter) and number of puppies alive at 14 days of age in a population of Boxers, using a repeatability animal model. Litter size was considered a trait of the dam and the model adjusted for fixed effects of contemporary group (breeder x birth year), litter sire, parity of the dam, the linear regression of dam age, the additive genetic effect of the dam and the permeant environmental effect of dam across her litters (Mostert et al. 2015). The heritability of litter size at birth was estimated to 0.23 and 0.25 for number of puppies alive at 14 days.

The previous heritability estimates of litter size mentioned above could be considered low to moderate. However, they are at an expected level when comparing to litter size heritability estimated in other species, such as pigs (h^2=0.11-0.12) (Ogawa et al. 2022), goats (0.06-0.19) (Heba et al. 2021), rabbits (0.07-0.10) (Badawy et al. 2019) and minks (0.08-0.17) (Madsen et al. 2020).

When selecting individuals for breeding, a selection based on estimated breeding values (EBVs) can lead to a faster genetic gain compared to a selection based on phenotype only (Arvelius & Klemetsdal 2013). This is arguably particularly relevant for multifactorial traits, where the variance of environmental factors leads to low heritability estimates. The EBV of a breeding animal statistically predicts the genetic contribution (of certain measurements covered by the EBV) that said animal will provide to a specific population via its offspring (Arvelius et al. 2013).

A best linear unbiased prediction (BLUP) is an EBV based on statistical mixed linear models. A BLUP-based evaluation is based on information about the performance of the dog itself as well as all available information on performance of its relatives, while simultaneously adjusting for systematic environmental effects (Arvelius et al. 2013). BLUP-based EBVs for traits of low to moderate heritability are available for several dog populations in Sweden today, e.g., as a tool for reducing the prevalence of hip dysplasia in 44 breeds (SKK 2021a) and in a breeding program aiming to increase curiousness and decrease nonsocial fear in the Collie breed (Eleryd 2020). Today there are no EBVs available for any trait in the Swedish population of Shetland Sheepdogs and the possibility to use BLUP-based breeding values to increase mean litter sizes in the breed has not previously been investigated.

Aim

The main aim of this retrospective study was to estimate the heritability of litter size in the Swedish population of the Shetland sheepdog breed. A secondary aim was to investigate the potential influence of various factors, such as maternal age and parity, birth year, birth month and inbreeding coefficients of the litter, dam and sire on the trait litter size.

2. Material and method

2.1 Data

The data used in this study was provided by SKK. The data included information on individual dogs of the Shetland sheepdog breed, registered in SKK during the time period from 1962 to 2021. Information on individual dogs' registration number, registered name, sex, date of birth and the registration numbers of the sires and dams were included in the dataset. The original data included observations from 39 933 individuals. R (version 4.1.2) was used to visualize, edit and create descriptive statistics from the dataset in the integrated development environment RStudio (version 2021.09.1) (R Core Team 2021).

The litter size variable was created by combining an individual's birth date with the registration number of its dam. Litters are normally registered in SKK before the age of 8 weeks. All puppies born and alive at the time of registration (within five months after the birth) must be registered, according to the statutes of the organization (SKK 2022). Stillborn puppies and puppies who die before the date of registration are not centrally registered and data of this kind were consequently not included in the study.

When considering the mean litter size per year in the original dataset a noticeable change in the mean was found after the year of 1975 (Figure 1). Because early data was considered unreliable, observations on litters born before the year 1980 were excluded, leaving data of litter size during 41 years (January 1980 - November 2021) from 10 443 unique litters.

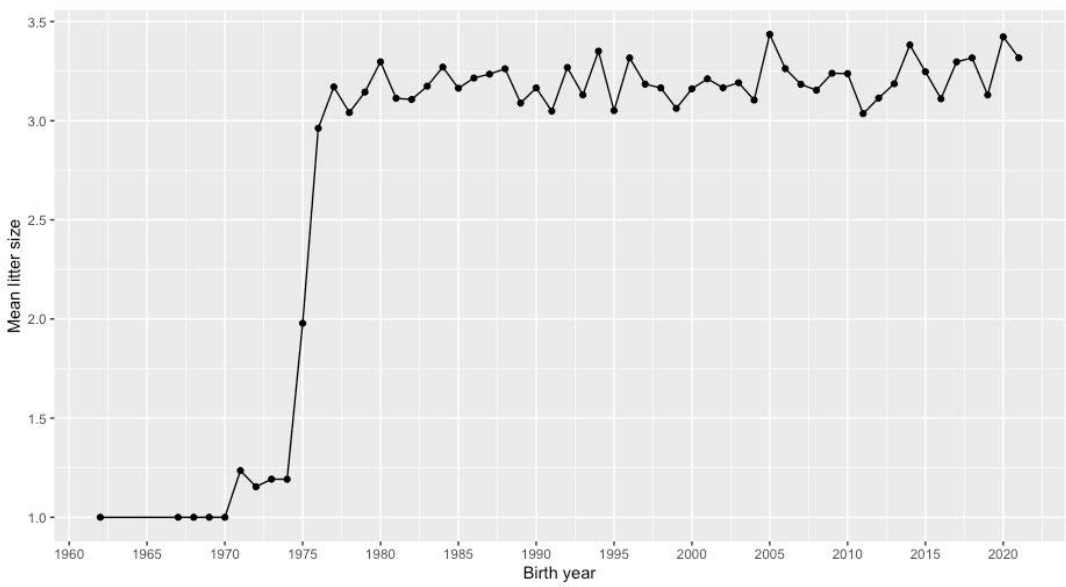

Figure 1. Mean litter size per birth year, from 1962 to 2021 for Swedish Shetland sheepdog.

2.2 Factors studied

To be able to adjust for environmental factors when estimating litter size heritability, the effect of litter birth year and month, as well as maternal age and parity was studied. Initial analysis showed no significant effect of birth year, which was excluded from further enquiry.

During initial analyses the effect of birth month showed a pattern across the year. Therefore, litters were grouped by birth season based on the meteorological seasons of the northern hemisphere, winter (December - February), spring (March - May), summer (June - August) and autumn (September - November).

Litters were divided into groups according to their mothers' age in years at the birth of the litter. Dam age was calculated in days, using her date of birth and the litter birth date. The age in days was then recalculated into age in years, defined as multiples of 365 days. The first and last age groups included few observations (Table 1). Therefore, litters were grouped into three categories depending on the age of the dam at the birth of the litter (Table 2).

Table 1. Number of litters (n) born and mean parity number (P) of dams of different ages (in years), between the years 1980 and 2021

	Age (years)											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
n	9	946	2625	2303	1762	1325	919	41	11	2	1	1
P	1.0	1.0	1.2	1.7	2.3	3.0	3.6	4.2	4.3	5.0	6.0	5.0

Table 2. Number of litters (n) born to dams of different age groups, between 1980 and 2021

	Age (years)		
	≤3	**>3 and ≤5**	**>5**
N	3580	4065	2798

Similarly, the dataset included few observations for litters born in a late parity (Table 3). Therefore, litters born in parity 7 and later were grouped together, creating a class of 22 observations. The parity variable was created by combining dam registration number and the birth date of her litters.

Table 3. Number of litters (n) born in parity 1 to 10, between the years 1980 and 2021

	Parity									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
N	4415	2837	1722	943	426	78	16	4	1	1

Inbreeding coefficients (F) for dams, sires and litters, were computed using the CFC software (Release 1.0) (Sargolzaei et al. 2006), allowing further analysis of a possible inbreeding effect on litter size. The PEDIG software (Boichard 2002) was used to compute an equivalent number of known generations of ancestors (EqG) as described by Boichard et al. (1997):

$$\mathrm{EqG}_j = \sum_{i=1}^{n^i} \frac{1}{2^{g_{ij}}}$$

where n_i is the total number of ancestors of animal *j* and g_{ij} is the number of generations between animal *j* and its ancestor *i*. Inbreeding information was saved in four different datasets. *Data_F* included the 1494 litters, where litters, dams and sires all had an F based on an EqG of two or more. *Data_litterF* included the 6164 litters where F_{litter} was based on at least two EqG. *Data_damF* included 4679 litters and *Data_sireF* included 2430 litters where F_{dam} and F_{sire}, respectively, were defined according to the same criteria.

2.3 Statistical analyses

The effect of the studied factors (birth year, birth season, dam age and parity) was tested for level of significance in a model where the additive genetic effect was excluded from model [1], using the *lmer* function (Bates 2005) in R and the dataset *Data_all*. Pairwise differences of classes within factors were tested using the *lsmeans* function (Lenth 2016) in R and mean litter sizes per class variables were estimated using the same function.

Statistical analyses were performed on the four different versions of the dataset with inbreeding data and one dataset that did not include information on inbreeding. This version, called *Data_all*, included data on all 10 443 litters. A mixed linear animal model was used to estimate breeding values (EBVs and associated standard errors (SE)), the heritability of litter size and different environmental effects using the AI-REML method in the DMU software (release June 4th 2021) as described by Madsen & Jensen (2013). The dependent variable of litter size was considered a trait of the mother in the model:

$$y_{ijklm} = \mu + bs_i + age_j + p_k + pe_l + a_l + e_{ijklm} \qquad [1]$$

where y_{ijklm} is the observed litter size (number of puppies alive at registration) of the *m*th litter of dam *l*; μ is the overall mean; bs_i is the fixed effect of birth season (*i* = winter, spring, summer, autumn) of litter *m*: age_j is the fixed effect of dam age in years at the birth of litter *m* (j = ≤3, 4 - 5, >5): p_k is the fixed effect of parity (k = 1, 2, 3, 4, 5, 6, ≥7); pe_l is the permanent random environmental effect of the dam *l* (~ND(0, $\mathbf{I}\sigma^2_{pe}$) where ND = normally distributed, **I** is the identity matrix and σ^2_{pe} is the permanent environmental dam effect variance; a_l is the random additive genetic effect of the dam *l* (~ND(0, $\mathbf{A}\sigma^2_a$) where **A** is the additive relationship matrix and σ^2_a is the additive genetic variance); and e_{ijklm} is the random residual effect of the observation y_{ijklm} (~ND(0, $\mathbf{I}\sigma^2_e$), where σ^2_e is the residual variance). Residuals were approximately normally distributed (Figure 2).

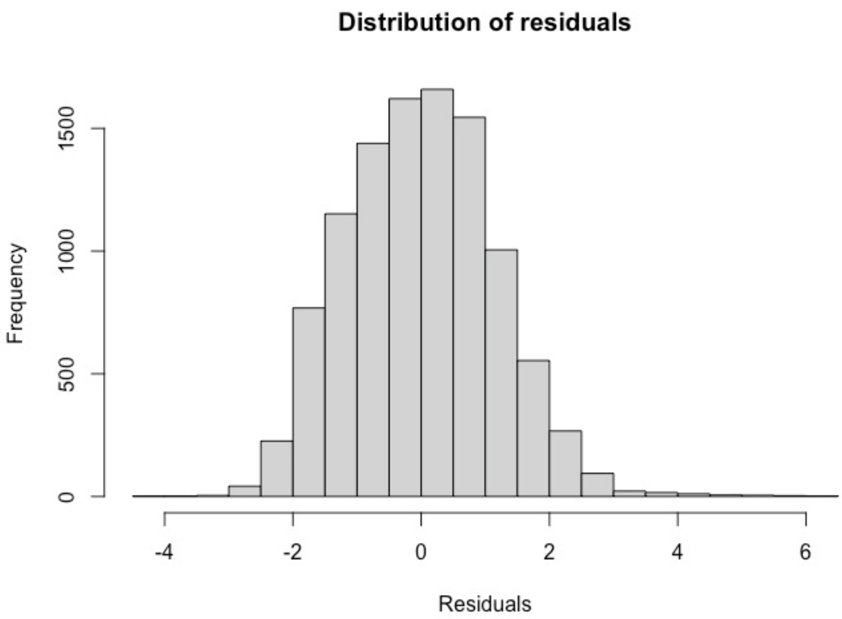

Figure 2. Distribution of residuals from model [1]

The other four datasets included, and were limited according to, inbreeding coefficient information. To estimate the litter size heritability when also correcting for all three inbreeding coefficients, using *Data_ F*, the following mixed linear animal model was used:

$$y_{ijklm} = \mu + bs_i + age_j + p_k + b_1F_{litter} + b_2F_{dam} + b_3F_{sire} + pe_l + a_l + e_{ijklm} \qquad [2]$$

where b_1F_{litter}, b_2F_{dam} and b_3F_{sire} are the linear regressions on inbreeding coefficients of the litter, dam and sire, respectively, and b_1, b_2 and b_3 are the regression coefficients. The remaining model corresponds to model [1]. The effect of the three inbreeding coefficients were also tested separately: F_{litter} when using *Data_litterF*, F_{dam} when using *Data_damF* and F_{sire} when using *Data_sireF*.

The heritability of the litter size trait was defined as

$h^2 = \sigma^2_a / (\sigma^2_a + \sigma^2_{pe} + \sigma^2_e)$

3. Results

3.1 Population structure

Approximately a third (33.8%) of the 10 443 litters registered between 1980 and 2021 were one- or two-puppy litters. Most litters born during the period had three (24.8%) or four (23.5%) puppies at registration (Table 4). The mean litter size per year has fluctuated between 3.0 and 3.4 puppies per litter during the same period (Figure 1).

Table 4. Number of litters (n) and litter frequency (%) per litter size, for litters registered in SKK between 1980 and 2021. No 11-puppy litters were registered during the time period

	Litter size										
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
n	1439	2086	2594	2455	1276	462	82	28	4	14	3
%	13.8	20.0	24.8	23.5	12.2	4.4	0.8	0.3	0.04	0.13	0.03

Although the number of litters born per year has fluctuated during the time period studied (from a minimum of 177 litters in 1981 to a maximum of 317 litters in 2007), a positive trend can be seen up until around 2008 (Figure 3).

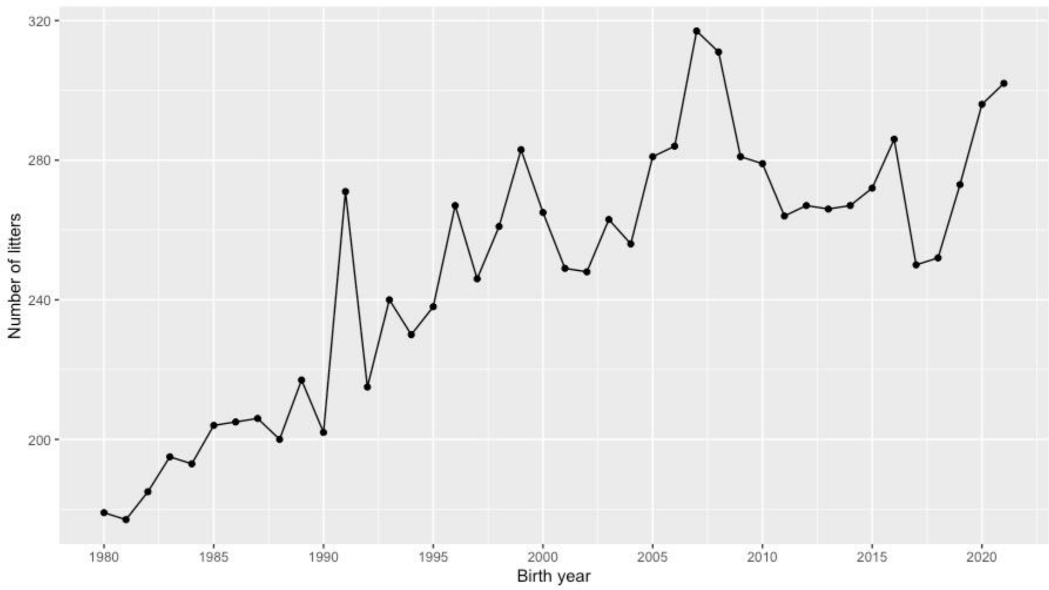

Figure 3. Number of litters registered per birth year, between 1980 and 2021 for Swedish Shetland sheepdogs. 10 443 litters were registered in total during the time period. Note that data from year 2021 only cover litters born in January to November.

Most of the registered litters were born in spring and the least number of litters were born in autumn (Table 5). Most dams were between 3 and 5 years old at whelping (

Table 6). Naturally, most litters (42%) were born in the first parity of the dam and the number of litters decreased with increasing parity (

Table 7). Similarly, the mean dam age increased per parity, being a mean of 3.3 years of age at the first parity and 8.2 years of age at parity 7 and above (not shown).

Table 5. Number of litters (n), litter frequency and least squares means of litter size ±SE per birth season, Winter (Dec-Feb), Spring (Mars-Apr), Summer (June-Aug) and Autumn (Sep-Nov)

	Birth season			
	Winter	**Spring**	**Summer**	**Autumn**
N	2288	3382	2604	2169
Frequency (%)	22	32	25	21
Mean litter size ±SE	3.16±0.06	3.17±0.06	3.14±0.06	3.07±0.06

Table 6. Number of litters (n), litter frequency and least squares means of litter size ±SE per dam age class. Dam age is defined as the age of the mother at whelping, in years

	Age class		
	≤3	**>3 and ≤5**	**>5**
N	3580	4065	2798
Frequency (%)	34	39	27
Mean litter size ±SE	3.36 ±0.07	3.19±0.06	2.85±0.05

Table 7. Number of litters (n), litter frequency and least squares means of litter size ±SE per parity. The last parity class includes litters born in parity 7 to 10 of the dam

	Parity						
	1	**2**	**3**	**4**	**5**	**6**	**≥7**
N	4415	2837	1722	943	426	78	22
Frequency (%)	42	27	17	9	4,1	0,7	0,2
Mean litter size ±SE	2.81 ±0.03	3.34 ±0.03	3.43 ±0.04	3.54 ±0.05	3.4 ±0.07	2.91 ±0.16	2.51 ±0.3

3.2 Factors studied

3.2.1 Effect of birth season, maternal age and parity

The effect of birth season was almost significant on the 5% level (P=0.055) whereas both maternal age and maternal parity had a highly significant effect on litter size (P<0.001). Effect of birth year was initially tested but was not significant.

The mean litter sizes were roughly the same during all four seasons, where litters were largest when born in spring and smallest when born in autumn (Table 5). Pairwise comparisons of the class variables (

Table 8) showed a significant difference between spring and autumn, but no difference between other seasons.

The three class variables of dam age were all highly significantly different from each other. Mean litter size decreased with increasing dam age where dams being 3 years old and younger had the greatest mean litter size. Dams who were over 5 years of age at whelping were the smallest age class with the lowest mean litter size (

Table 6). Mean litter sizes increased in parity 2 to 4, then decreased in the following parities. Litters were largest when born in parities 3 to 5 and smallest when born in parity 7 and later (

Table 7). The first parity differed significantly from parity 2, 3, 4, and 5, but not from 6 and 7.

*Table 8. Pairwise comparisons of factor class variables of birth season, dam age and parity for Swedish Shetland sheepdogs (values are row estimate – column estimate). The estimated difference in mean litter size between classes ±$_{SE}$ is presented with significance levels '***'0.001, '**'0.01, '*'0.05, '.'0.1*

Factor			*Class variables*				
Birth season				*Spring*	*Summer*	*Autumn*	
			Winter	$-0.018_{0.04}$	$0.021_{0.04}$	$0.084_{0.04}$	
			Spring	---	$0.039_{0.04}$	$0.102_{0.04}^{*}$	
			Summer		---	$0.064_{0.04}$	
Dam age in years				*>3 x ≤5*	*>5*		
			≤3	$0.169_{0.04}^{***}$	$0.513_{0.05}^{***}$		
			>3 x ≤5	---	$0.344_{0.04***}$		
Parity		*2*	*3*	*4*	*5*	*6*	*≥7*
	1	$-0.531_{0.04}^{***}$	$-0.619_{0.05}^{***}$	$-0.727_{0.06}^{***}$	$-0.59_{0.08}^{***}$	$-0.096_{0.16}$	$0.299_{0.3}$
	2	---	$-0.088_{0.04}$	$-0.196_{0.06}^{**}$	$-0.059_{0.08}$	$0.435_{0.16}$.	$0.83_{0.3}$.
	3		---	$-0.108_{0.05}$	$0.029_{0.07}$	$0.523_{0.16}^{*}$	$0.918_{0.3}^{*}$
	4			---	$0.137_{0.08}$.	$0.63_{0.16}^{***}$	$1.026_{0.3}^{**}$

5	---	$0.494_{0.16}$*	$0.889_{0.3}$*
6		---	$0.395_{0.33}$

3.2.2 Effect of inbreeding coefficients

Effects of all inbreeding coefficients are shown in Table 9. The inbreeding coefficient of the sire had a significant and positive effect on litter size when using the dataset *Data_F* (Figure 4) but showed no significance when only F_{sire} was included in the model, using *Data_sireF*. When only F_{litter} was adjusted for, using *Data_litterF,* the effect was negative and significant (Figure 5). The effect of F_{litter} was negative but not significant when also adjusting for F_{dam} and F_{sire} in the model. The inbreeding coefficient of dam had nonsignificant negative effect on litter size. Less than 10% of the litters, dams and sires had an F of 0.0625 or more (not shown).

*Table 9. Effects of inbreeding coefficients (F) on the litter size trait. Estimation±SE, n=number of litters, *significant effect (P < 0.05)*

Dataset	**F litter**	**F dam**	**F sire**	**n**
Data_litterF	-1.6±0.6*			6164
Data_damF		-1.1±0.9		4679
Data_sireF			1.3±0.9	2430
Data_F	-0.6±1.1	-2.1±1.5	2.7±1.2*	1494

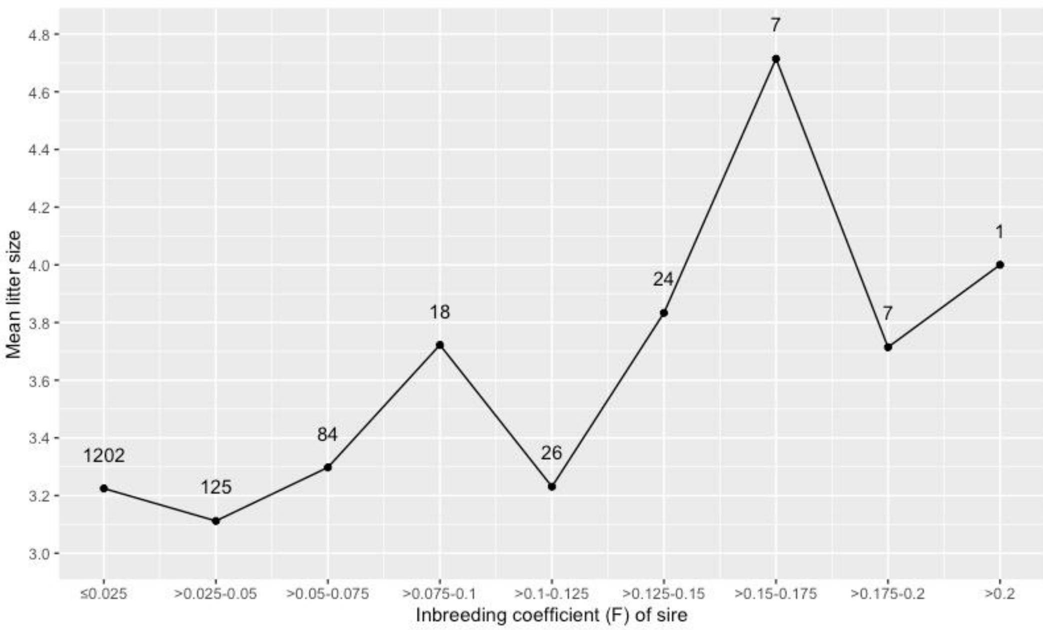

Figure 4. Mean litter size per sire inbreeding coefficient (F) category. Data is derived from Data_F with a total of 1494 litters. Number of litters per category is given above the dots.

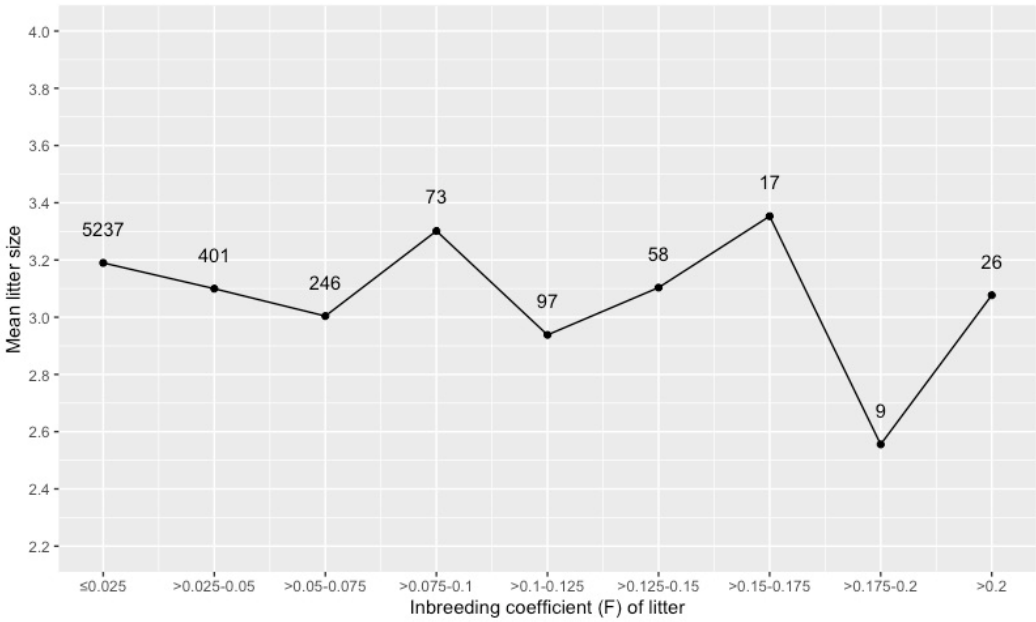

Figure 5. Mean litter size per litter inbreeding coefficient (F) category. Data is derived from Data_litterF with a total of 6164 litter observations. Number of litters per category is given above the dots.

3.2.3 Estimated heritability

The estimated heritability (h^2) of litter size differed depending on the dataset used (Table 10). The highest h^2 was estimated using *Data_F*, where F of litter, dam and sire were all adjusted for in the model. This dataset included the least number of litters. Similarly, the next smallest dataset *Data_sireF* had the next highest estimated h^2. Including only F_{dam} and F_{litter}, respectively, in the model gave the lowest estimates of h^2. When no inbreeding coefficients were adjusted for in the model, using *Data_all* with the greatest number of litters, h^2 was estimated to 0.15. This estimate also had the lowest SE.

Table 10. Estimates of litter size heritability (h^2) and variance components±SE. σ^2_a=additive genetic variance, σ^2_{pe}=permanent environmental dam effect variance, σ^2_e=residual variance, n=number of litters

Dataset	**h^2**	**SE**	**σ^2_a**	**σ^2_{pe}**	**σ^2_e**	**n**
Data_all	0.150	0.018	0.31±0.04	0.18±0.04	1.58±0.03	10 443
Data_litterF	0.135	0.022	0.27±0.04	0.24±0.05	1.46±0.04	6164
Data_damF	0.140	0.025	0.29±0.05	0.17±0.05	1.60±0.04	4679
Data_sireF	0.194	0.040	0.39±0.08	0.22±0.09	1.39±0.06	2430
Data_F	0.223	0.052	0.46±0.11	0.09±0.11	1.50±0.09	1494

Individuals that could potentially be relevant for selection and thereby contribute genetically to the next generation were considered to be born no earlier than 2010. Mean accuracy (r_{TI}) was therefore calculated for individuals born between 2010 and 2021 (r_{TI}=0.38, n=10 570). Accuracy is the correlation between the true and the estimated breeding value, calculated from $r_{TI}^2=1-(PEV/\sigma^2_a)$, where *PEV* is the prediction error variance (SE^2) derived from the DMU estimation (model [1]) and σ^2_a is the estimated additive genetic variance (here 0.3124657). Mean r_{TI} was also calculated for dams with one litter (r_{TI}=0.50, n=449), dams with more than one litter (r_{TI}=0.61, n=513) and bitches that had not given birth to any litter (r_{TI}=0.36, n=9608). Because litter size was defined as a trait of the dam, the latter calculation (r_{TI}=0.36) could also be assigned to male dogs.

When considering the genetic trend over time by plotting mean EBV for litter size (derived from model [1] using *Data_all*) per birth year, a positive trend was noticeable from the year of 2011 (Figure 6).

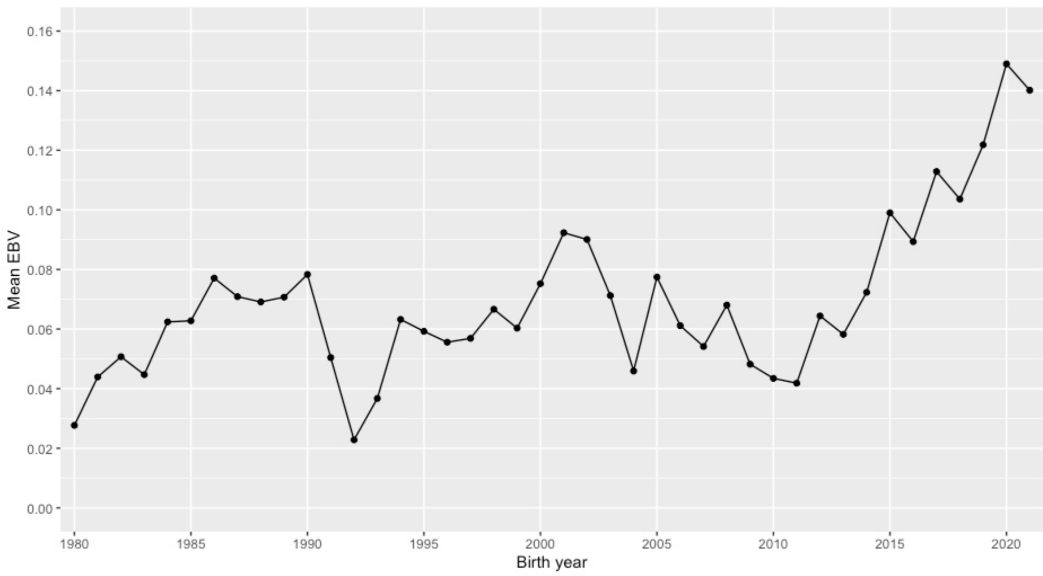

Figure 6. Mean EBV per birth year for Swedish Shetland sheepdogs born between 1980 and 2021.

4. Discussion

The number of Shetland sheepdog litters registered in SKK has increased successively since the year of 1980, reaching a peak in number of registered litters per year in 2007 (Figure 3). The trend visualised in Figure 3 indicates that the number of litters registered per year has reached a current plateau.

In this study, litter size observations from the earliest years were excluded from the original dataset due to unreliable data. Between 1962 and 1975 mean litter sizes fluctuated between 1.0 and 2.0 puppies per litter, whereas the mean was between 3.0 and 3.4 puppies per litter during the period from 1977 to 2021. It is possible that only individuals kept for breeding were registered in SKK during the earliest years of registration. This hypothesis would explain the abrupt change in mean litter sizes shown in Figure 1. When excluding data from the earliest years, the study still covered 41 years of observations, exceeding the number of years covered in three previous studies on litter size heritability, where heritability data covered 22 (Leroy et al. 2015), 24 (Mostert et al. 2015) and 33 years (Hare & Leighton 2006) respectively.

4.1 Factors affecting litter size

Birth year and birth season

Birth year was initially included as a fixed effect in the mixed linear model. In accordance with previous study results (Kania-Gierdziewicz & Pałka 2019; Schrack et al. 2017; Hare & Leighton 2006), the effect of birth year on litter size was not significant in the present study and was therefore excluded from the final models. In contrast, birth year did have a significant positive effect on litter size in a population of Dutch Kooiker dogs (Mandigers et al. 1994). However, the data of that study included dogs born between 1956 and 1990, and the increase in litter sizes over time was likely largely due to environmental factors, such as a general increase in living standards and pet food quality. Regarding the relatively constant mean litter size per year in the Shetland sheepdog population, the nonsignificant effect of birth year on litter size was expected.

In the present study birth season almost had a significant effect on litter size ($P=0.055$), but only spring and autumn were significantly different from each other ($P<0.05$). Mean litter sizes were larger by 0.1 puppy when born in spring compared to autumn. Most of the litters were also born in spring (32%) and least (21%) in autumn, which possibly could be explained by breeders adapting their breeding practises to a higher demand for puppies during spring and summer. A similar result was seen in 224 litters of Drever dogs bred in a private kennel in Sweden (Gavrilovic et al. 2008). However, when including 2717 litters from the larger Drever population registered in SKK, no effect of birth month was found in that study and the result was assigned to the specific living and breeding conditions in the private kennel. A study on German Shepherd dogs showed reversed results, where mean litter sizes were largest in autumn (November) and smallest in spring (April) (Šichtař et al. 2016). According to Lord et al. (2013) the domestic dog is not a seasonal reproducer, in contrast to other wild canine species, which could partly be attributed to the constant supply of recourses provided by humans, such as food and shelter.

Only small differences in number of litters and mean litter sizes per season were found in the Shetland sheepdog population. This indicates that the population does not have a strong seasonal reproductive pattern. Furthermore, it could be argued that the positive effect of birth season presented in this study was not prominent enough (0.1 puppy per litter, adjusted for dam age and parity) to recommend seasonally based breeding.

Dam age and parity

When dividing litters according to dam age in years at whelping, the youngest and oldest dam age classes had few observations. To get a more even number of observations per class variable, classes were grouped together into three groups corresponding to young, adult and older dams. The mean litter size declined with increasing dam age class and the classes were highly significantly ($P<0.0001$) different from each other. A decrease of almost half a puppy in mean litter size could be expected for dams older than 5 years compared to dams aged 3 years and younger, adjusted for parity.

Because classes for dams of age 1 and 2 years almost only included first parity litters (Table 1), the factors of dam age and parity overlapped, creating a confounding effect. By dividing the age classes into three bigger groups, the confounding effect of parity could be partly avoided. Previous studies on dog litter size have handled the confounding issue between parity and dam age in different ways. In a study by Schrack et al. (2017) where different explanatory variables for the litter size trait and puppy losses in the Entlebucher Mountain dog were analysed, parity and dam age were found to be strongly correlated. The authors decided to exclude parity from the model completely, since there were only a few dams who had given birth to more than two litters, making the weak but significant negative effect of dam age a more reliable explanatory variable (Schrack et al. 2017). Borge et al. (2011) who studied environmental factors affecting litter sizes in 224 dog breeds, did see a negative effect of parity on litter size in their initial analyses of unconditional association. However, when both parity and dam age were included in the multivariable analysis, parity did not show a significant effect on litter size.

Further analysis showed that the initial negative effect of parity was rather due to the increasing dam age (Borge et al. 2011). When parity was not adjusted for in that study, dam age had a negative effect on litter size in larger breeds, while litter sizes in small breeds were smaller when dams were young and old, compared to ages in between.

Dog litter sizes have previously been found to be largest when born in parity numbers 2 to 3 (Leroy et al. 2015). That study did however not adjust for dam age in the statistical model. In a study by Šichtař et al. (2016), parity did have a significant effect on litter size when adjusting for dam age, with the largest litters being born to dams of parity 2 to 5. The biggest litter sizes were found in parities 3 to 5 in the present study, whereas both lower and higher parities had about 0.5 to 0.9 fewer puppies, adjusted for dam age.

Primiparous dams of older age (four to six years and older) have previously been associated to smaller litters as well as higher incidence of dystocia compared to dams giving birth to their first litter at a younger age (Münnich & Küchenmeister 2009; Gavrilovic et al. 2008). In the present study, the first parity was highly significantly different compared to all but parity 6 and 7. Analyses in the present study showed that both parity and dam age, when grouped into three classes, had a highly significant effect on litter size ($P<0.001$).

Inbreeding coefficient of litter, dam and sire

To be included in the model [2] analysis in the present study, litters had to have at least 2 equivalent generations of known ancestors (EqG). In previous studies this criterion, and the means of calculating EqG, has varied. In a study on the Swedish population of Irish Wolfhounds, litters had to have a complete pedigree over seven or more generations to be included (Urfer 2009). In a study by Leroy et al. (2015), where the method for calculating EqG corresponded to the present study, litters had to have at least 3 EqG to be included.

If the criterion was set to at least 3 EqG instead of 2 in the present study, a considerable amount of litter data would be lost from all five datasets. *Data_litterF* would decrease with 3310 litter observations (from 6164 to 2854) when limiting the data from 2 EqG to a criterion of at least 3 EqG. *Data_damF* would decrease with 2629 observations (from 4679 to 2044 litters), *Data_sireF* with 1439 observations (from 2430 to 991) and *Data_F* with 1099 observations (from 1494 to 395 litters). It is common that imported individuals are used for breeding in the Swedish Shetland sheepdog population. According to the breed-specific breeding strategy, approximately 80% of the litters registered in SKK between 1990 and 2018 had at least one grandparent that was born outside of Sweden (SSSK, 2019). By keeping all litters with at least 2 EqG, more litters with non-Swedish ancestry could be included in the analysis.

In this study, the inbreeding coefficient (F) of the sire had a significantly positive effect on litter size, when also adjusting for litter and dam inbreeding. This is opposite to the expectation from the theory assuming dominance as a reason for inbreeding depression. In a study on litter size in the Dutch Kooiker dog breed, a similar positive, but nonsignificant, association was found between the level of sire inbreeding and litter size (Mandigers et al. 1994). According to the authors, the estimated effect of sire F was likely the result of many litters being sired by 12 highly inbred and inter-related individuals with a familial genetic background that was beneficial for litter size.

Two possible explanations for the unexpected association between sire inbreeding and litter size in the present study were investigated. One hypothesis was that highly inbred sires were mated with dams who, by chance, were genetically predisposed to give birth to bigger litters. This was tested by giving highly inbred sires ($F_{sire} \geq 0.125$, corresponding to a mating between half siblings) the indicator 1, and less inbred sires the indicator 0. Mean EBVs for litter size of the group of dams mated with indicator 1 sires was then compared to the mean EBVs of dams mated with indicator 0 sires, using the *lm* function (Prabhakaran 2017) in R. Dams mated with sires of an F lower than 0.125 had a mean EBV of 0.06, whereas dams mated with more inbred individuals had a mean EBV of 0.13. Although the difference is in line with the hypothesis, the effect was not significant. The difference between litter size was also tested between the two indicator groups, using the same method. Sires with a high F (≥ 0.125) had a significantly ($P<0.05$) higher litter size by about 0.5 puppies compared to litters sired by individuals with lower F. The unexpected positive correlation between F_{sire} and litter size is therefore likely due to a sire outlier effect, which could be discerned in Figure 4.

Level of dam inbreeding had a negative effect on litter size in several previously studied dog populations (Andrade et al. 2021; Chu et al. 2019; Schrack et al. 2017; Leroy et al. 2015; Urfer 2009). When litter sizes are defined as number of puppies alive at registration, the measurement will cover dam-related traits influencing embryo and neonatal survival (Leroy et al. 2015). Level of dam inbreeding could consequently be expected to affect litter size negatively. The effect of dam inbreeding in this study was negative but nonsignificant. This is in accordance with a study by Kania-Gierdziewicz & Pałka (2019) showing that neither parental nor litter inbreeding had a significant effect on litter size in any of the five dog breed populations studied. According to the authors, those results were likely due to the low frequency of inbred ($F>0.0625$) litters included in the study, as well as generally low inbreeding coefficient values for dams and sires. In a study on Irish Wolfhounds dam inbreeding had a significant effect on litter size when estimated over 30 generations as well as over the whole pedigree (Urfer 2009). Since the mean inbreeding coefficient of dams were over 0.3 for both definitions (Urfer 2009) the effect was rather expected. In the present study, the frequency of dams with an inbreeding coefficient lower than 0.0625 was approximately 94% which may explain the nonsignificant effect on litter size. In fact, less than 10% of litters, dams and sires had an inbreeding coefficient of 0.0625 or more in the Shetland sheepdog population. This could indicate that breeders of the population are careful about breeding two individuals that are closely related to each other, which is in accordance with the recommendations from SKK stating that the inbreeding level of a litter should not exceed 6.25% (SKK 2014).

4.2 Heritability

The scientific studies on heritability of litter size in dogs are limited and results from three such studies have been presented in the introduction of this thesis. In agreement with the results from these previous studies, the heritability of the litter size trait in the present study was estimated from 0.14 to 0.22, which could be considered low to moderate value, as is expected for a multifactorial trait. The definition of litter size used in the present study corresponds to that of Leroy et al. (2015) where heritability estimates ranged from 0.06 to 0.11 in the seven breeds included. Data from the different breeds ranged in size, from the smallest dataset including observations from 3246 litters (Leonberger) to the biggest including 39 080 litter observations (German shepherd dog) (Leroy et al. 2015). The authors discussed that the low estimated heritability may be the result of a low number of litters per dam, sire and breeder, making it difficult to adjust the genetic models.

Of the four definitions of litter size in the study by Hare & Leighton (2006) the one corresponding best to the definition used in the present study is number of puppies alive at the age of 49 days. The heritability for this litter size definition was estimated to 0.31 in the Labrador retriever population and 0.26 in the German shepherd dog population. The estimates were based on data from 618 and 703 litters, respectively. As discussed by the authors, these higher estimates can likely be attributed to the standardized living environment at the service dog breeding colony, where the dams lived, gave birth to and reared their litters, minimizing environmental variability. In contrast to the study by Leroy et al. (2015), the study by Hare & Leighton (2006), as well as the present study, included a higher frequency of dams producing more than one litter. These repeated measures may further explain the higher heritability estimations compared to the study by Leroy et al. (2015). However, a study on litter size heritability in a Boxer breed population yielded higher heritability estimates of 0.23 and 0.25, even when only 25% of the litters included were born from dams who produced more than one litter in total (Mostert et al. 2015).

The highest heritability estimated in the present study, of 0.22, was calculated from the smallest dataset where F_{litter}, F_{dam} and F_{sire} all were adjusted for in the statistical model. However, when all inbreeding coefficients were excluded from the model, using the same dataset, the estimated heritability was still 0.22. The high estimate can therefore be assigned to the specific data, rather than taking the level of inbreeding into account in the estimation. The standard error was also largest for this estimate. Thus, the most reliable estimate of heritability is expected to be that from the largest dataset in our study (h^2=0.15), which also had the lowest SE.

4.3 Genetic progress and selection

The genetic progress per generation, defined as $i\ r_{TI}\ \sigma_A$, was calculated for the bitches and male dogs who represented the 20% of the individuals born between 2010 and 2021 with the highest EBVs for litter size (selection intensity (*i*) =1.4). The accuracy was calculated as a mean of the r_{TI} for dams that had one previous litter (0.5) and for bitches without any previous litter (r_{TI}=0.36), which here represents the male dogs. If only these individuals would be selected for breeding, the genetic breeding progress would be 0.34 per generation. It is, in other words, theoretically possible to increase average litter size in the population by a third of a puppy for every generation.

The accuracy when using a BLUP-based selection for dams with one litter (0.5) was greater than what was expected from a selection based on phenotype only ($\sqrt{h^2}$=0.39). The added information from the relatives in the BLUP evaluation increased the accuracy of the prediction. This is in accordance with a prediction of accuracy for EBVs of a low heritability (h^2=0.11) trait in the Border Collie (Arvelius et al. 2013).

Even though a genetic progress for the litter size trait in the Swedish Shetland sheepdog population is theoretically possible, the success rate depends on implementation. The result of this study suggests that a BLUP-based breeding value is a suitable tool for improving Shetland sheepdog litter sizes. EBVs are generally easy for dog breeders to understand and use (Arvelius et al. 2013). In addition, BLUP-based EBVs are already implemented in breeding programs for other SKK registered breeds, which could make the possible gap in selection practise easier to bridge. A breeding practice aiming to increase litter sizes could be facilitated for Shetland sheepdog breeders by creating a litter size index, similar to the one used for selection against hip dysplasia in other breeds (SKK 2021a).

When the genetic progress was predicted, only litter size EBV was considered as basis for selection. However, the selection of breeding animals is also based on other traits, such as conformation, temperament, availability and results from dog shows and other tests and competitions. How the litter size trait is prioritised compared to other selection traits will affect the efficiency of the genetic progress. If breeders of Swedish Shetland sheepdogs want to increase litter sizes in the population, it is important that they have similar breeding goals, prioritising the trait equally.

If a litter size index would be implemented in a breeding program for the Shetland sheepdog population, it would be important to evaluate the effect continuously. This is especially crucial since possible negative genetic correlations between litter size and other desired traits is not yet established, a concern also raised by Hare & Leighton (2006). The positive genetic trend for litter size per birth year since the year of 2011 (Figure 6), could indicate that the litter size trait is positively genetically correlated to other desired traits that constituted the basis of breeding animal selection. In theory, it could also indicate that selection have been based on phenotypic litter size during this period. Regardless, the genetic correlation between litter size and other desired traits for the Shetland sheepdog needs to be further studied to be able to draw accurate conclusions.

Another reason for continuous evaluations of a breeding programme aiming to increase litter sizes in the Shetland sheepdog is being able to define an optimal litter size. It is possible that a great increase in mean litter sizes have other negative effects. For instance, large litters, as well as small, are associated with dystocia (Cornelius et al. 2019). Furthermore, as discussed by Hare & Leighton (2006), it is not known how an increase in litter sizes may affect the living environment and development of the puppy. The results presented in this study confirm previous conclusions (Marelli et al. 2020; Leroy et al. 2015) that reproductive performances in canine populations could be improved if different fertility measurements, such as litter size EBVs, are included in the selection of breeding animals.

4.4 Study limitations

In this study, litter size was defined as the number of puppies per litter alive at the age of registration. Although registration normally occurs before the age of 8 weeks, when puppies are generally weaned, the registration in SKK could occur up until a litter age of 5 months. Consequently, the data presented in this study does not cover stillbirths or early puppy mortality. Information on the prevalence of unsuccessful matings were also missing.

In 2018 the Swedish Shetland sheepdog breed club sent a questionnaire to their breeders, asking about litter sizes and puppy mortality (SSSK 2019). The questionnaire was answered by 74 breeders and covered information about 303 litters, mainly born in 2016-2018. According to the questionnaire about 11% of the litters had no surviving puppies, and in 30% of the litters there were at least one puppy who did not survive until registration. Most non-surviving puppies were born in one- or two-puppy-litters, and almost 60% of all non-surviving puppies were born dead (SSSK 2019). The result of this questionnaire is not scientifically validated, and it covers a small number of litters. However, it gives insight into data that was not covered by the present study and sheds some light on possible puppy mortality problems in the population.

The result of the breed club questionnaire indicated that puppy mortality is not the main reason for small litter sizes in the Shetland sheepdog population, since roughly 30% of the litters described in the questionnaire were one- or two-puppy-litters (SSSK 2019), which corresponds to the present study result of registered litter sizes (Table 4). Still, the incidence of puppy mortality and other fertility related traits in the Swedish population of Shetland sheepdogs should be further investigated in future studies.

4.5 Conclusion

This is the first study estimating the heritability of litter size in the Swedish Shetland sheepdog population. The estimated heritability was rather low (0.15), which could be expected for a multifactorial trait with a comparably low mean. Yet, a theoretical estimation of breeding progress for the trait showed that it is possible to select for bigger Shetland sheepdog litters with the use of best linear unbiased prediction (BLUP) based breeding values. The success rate if implementing a BLUP-based selection tool will depend on the breeding goals of Shetland sheepdog breeders. Reaching efficient progress in the population requires breeders to have similar breeding goals, where the litter size trait is equally prioritised. Negative genetic correlations between litter size and other desired traits are unknown and a selection based on other traits could therefore lead to an unintentional decrease in litter sizes in the population. Regardless of priority, breeders are therefore encouraged to considering the litter size trait when selecting animals for breeding, thus supporting sustainable breeding of the Shetland sheepdog.

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Populärvetenskaplig sammanfattning

Hundrasen Shetland sheepdog är den sjätte vanligaste rasen i Sverige. Det är en allsidig ras som används såväl till sällskap som träning och tävling inom olika hundsporter och efterfrågan på Shetland sheepdog valpar är stor. Medelkullstorleken i rasen, på omkring 3 valpar per kull, har dock varit kontinuerligt låg jämfört med hundraser av liknande storlek. Svenska Shetland Sheepdog Klubben har uttryckt en önskan om att undersöka möjligheten för att, via avel, öka kullstorlekarna i populationen. Syftet med denna studie var att skatta arvbarheten för egenskapen kullstorlek, definierad som antal levande valpar per kull vid registrering i SKK. Kullstorlek är en egenskap som både påverkas av genetiska och miljörelaterade faktorer, och fördelningen av dessa avgör hur mycket av egenskapen som nedärvs till nästa generation. Det är detta som kallas arvbarhet. Studien syftade också till att undersöka hur olika miljöfaktorer, som tidigare visats vara kopplade till kullstorlek, påverkade egenskapen. I studien användes data från 10 443 Shetland sheepdog kullar födda och registrerade i SKK mellan åren 1980 och 2021.

Resultatet från studien visade att kullar födda på våren var 0.1 valp större i genomsnitt, jämfört med kullar födda under hösten. Kullar som föddes till mödrar som var äldre än 5 år var i genomsnitt 0,5 valpar mindre jämfört med kullar som föddes till mödrar som var 3 år och yngre. Även kullnummer påverkade kullstorleken och flest antal valpar observerades i mödrarnas andra till femte kull. En viss positiv påverkan av faderns inavelsgrad observerades, samt en viss negativ påverkan av kullens inavelsgrad. Arvbarheten skattades till 0,15, vilket anses vara ett lågt men förväntat värde. En teoretisk skattning av det genetiska framsteget kunde göras med hjälp av skattade avelsvärden för individerna i rasen. Det genetiska framsteget visar hur mycket kullstorleken kan förväntas förändras per generation, givet att vissa selektionskriterier möts. Om de hanar och tikar födda mellan år 2010 och 2021 med de 20% högsta avelsvärdena för kullstorlek skulle användas i avel, kunde en ökning av en tredjedels valp i snitt per kull förväntas på en generation. I verkligheten selekteras dock avelsdjur baserat på flera olika kriterier, däribland mentalitet, tillgänglighet och utställnings- och tävlingsresultat. Selektionen för ökade kullstorlekar skulle underlättas om BLUP-baserade avelsvärden införs i avelsprogrammet för Shetland sheepdog. Om ett avelsframsteg för kullstorlek ska kunna ske i rasen är det dock viktigt att uppfödare av Shetland sheepdog har ett gemensamt avelsmål, där egenskapen prioriteras på liknande sätt. Oavsett prioritet så bör kullstorlek tas i beaktande vid selektionen av avelsdjur, för att inte riskera att omedvetet minska medelkullstorleken i populationen.

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