Calving Performance in the Endangered Murboden Cattle Breed: Genetic Parameters and Inbreeding Depression

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Summary

Calving is a key event on any cattle farm, with both economic and animal welfare consequences when complications arise. Although mostly reported in highly selected breeds, problematic calving performance is also a worry to the unselected dual-purpose Murboden breed, local to Austria. This study presents genetic parameter estimates for calving ease and stillbirth in Murboden cattle. Furthermore, a potential effect of inbreeding on the breeds' calving performance is evaluated. Results show a moderate direct and maternal heritability (0.18±0.04; 0.11±0.02) and a significant negative direct-maternal genetic correlation for calving ease (-0.41±0.10). Heritabilities of stillbirth are low yet significant (0.048±0.01; 0.018±0.007). A significant effect of inbreeding was detected on maternal calving ease i.e. the ease with which a dam calves. By categorizing the inbreeding coefficients of the dam in six ascending classes it was shown that calving ease worsens as inbreeding coefficients become larger. Results of this study reveal significant genetic variation in calving performance of the Murboden breed which opens doors for genetic selection. An additional important aspect of this study is that its result on inbreeding depression gives counterweight to the general intuitive notion in literature that high selection for production traits is the major contributor to calving difficulty in dairy and beef cattle breeds worldwide.

Key words

calving ease, stillbirth, inbreeding depression, Murboden

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Aim

For a number of years, Austrian Farmers of the local Murboden cattle breed have been following a strict compulsory mating advice programme which is supported by state subsidies and organised by the Austrian Association for Rare Endangered Breeds (ÖNGENE 2008). By restricting the co-ancestry between mates, inbreeding coefficients of the next generation are kept low which consequently ensures a decrease in inbreeding rate and an increase in effective population size. Success of the programme is demonstrated by the fact that the effective population size of the Murboden population has grown considerably. Actually, the population has grown to such a size that, alongside mating on low co-ancestry, the estimation of breeding values and thus genetic selection has become a possibility.

Murboden farmers mainly express interest for genetically improving calving performance in their breed, despite that it is mostly kept for beef (ÖNGENE, 2008). Calving is a key event on any cattle farm with consequences of poor calving extending from high veterinary costs to reduced performance, compromised animal welfare and even the loss of individuals (Eaglen et al., 2011). Currently, high prevalence of difficult calving is identified in beef and dairy cattle breeds worldwide (Ramirez-Valverde et al., 2001; Eaglen et al. 2011). As a consequence, most large dairy cattle breeds publish estimated breeding values for both calving ease (CE) and stillbirth (SB) (Interbull, 2013). This study however shows that calving problems are not limited to large cattle breeds which undergo intensive selection. A first attempt to estimate genetic parameters for CE, SB and gestation length in Murboden was carried out by Manatrinon et al. (2009). However, at this time only a restricted number of records was available. This study attempts to estimate the genetic parameters for calving performance for a second time, using the current much larger dataset. Additionally, this study considers a potential influence of inbreeding on calving performance thereby addressing the paucity on studies assessing calving performance problems from a different angle than the one most commonly taken in literature: high selection on production traits.

Material and methods

25,154 Murboden calving records were provided by ZuchtData EDV-Dienstleistungen GmbH, Vienna, Austria and collected between 2000 and 2013. The raw dataset consisted of in total records representing 737 herds. Data contained records from 737 herds, offspring of 845 sires and 7267 dams and grand offspring of in total 414 maternal grandsires (MGS). Data were checked on inconsistencies and apparent errors in SAS v9.1 (SAS Institute, 2006) and restricted to single births only, representing parities 1-10. Contemporary groups were restricted to a minimum number of 3 records/sire, 3 records/MGS and 3 records/herd*year. Records showing a gestation length of >299 days were discarded to avoid the risk of recording errors and confusion between parities. The minimum gestation length recorded was 267 days. Potential abortions were therefore considered unlikely.

Table 1. Calving ease and stillbirth frequencies

	Frequencies			
	All calves			Stillborn
	Total	1st parity	>1nd parity	calves
1. Easy	70.38%	57.16%	74.51%	47.09%
2. Normal	23.94%	31.20%	21.44%	24.60%
3. Difficult	5.43%	10.91%	3.94%	26.05%
4. Caesarean	0.25%	0.73%	0.11%	2.27%
0. Alive	96.7%	93.07%	97.75%	0%
1. Stillborn	3.3%	6.93%	2.25%	100%

Approximately 50% of the records had a missing value for gestation length. Age of dam at calving ranged from a minimum of 16 months (1st parity) to a maximum of 162 months (10th parity). CE was recorded on a 5 grade scale, ascending in difficulty. The five CE categories were defined as: 1. Easy; 2. Normal; 3. Difficult; 4. Caesarean and 5. Embryotomy. As the last category, embryotomy, is likely caused by different genetic factors than the remaining categories, this category is dismissed from the study. SB is the calf performance trait which is most often associated with calving ease. Austria scores SB at birth, and mortality within 48 hours as different categories. Frequencies within these two categories however were too low for statistical analyses and categories were therefore merged according to the routine Austrian/German genetic evaluation (Fürst and Fürst-Waltl, 2006). The final dataset consisted of 17,175 records, originating from 414 herds and representing 450 sires, 313 MGS and 5,919 dams, with an accompanying pedigree of ~ 260,000 individuals (10 generations deep). In total, 3,955 of the calving records originated from first parity calvings. Table 1 presents the CE frequencies in the edited dataset alongside the SB frequencies and CE frequencies in the stillborn calves which demonstrates the strong phenotypic relationship between the two traits.

Both CE and SB are maternal traits, meaning that the phenotype is affected by both the calf (direct effect, ease of birth) and the dam (maternal effect, ease of calving). Both the direct and maternal effect consist of an environmental and genetic component. The direct-maternal genetic covariance represents the genetic relationship between an animal's ease of birth (as a calf) and ease of calving (as a dam, when female). Variance components were estimated with a linear bivariate animal model using ASREML (Gilmour et al., 2006).

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}X_1 & 0\\ 0 & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{d\_1} & 0\\ 0 & \mathbf{Z}_{d\_2}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{d\_1}\\ \mathbf{a}_{d\_2}\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{m\_1} & 0\\ 0 & \mathbf{Z}_{m\_2}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{m\_1}\\ \mathbf{a}_{m\_2}\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{hy} & 0\\ 0 & \mathbf{Z}_{hy}\end{bmatrix}\begin{bmatrix}\mathbf{h}_{hy\_1}\\ \mathbf{h}_{hy\_2}\end{bmatrix}+\begin{bmatrix}\mathrm{pe}_1\\ \mathrm{pe}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$$

where, $\mathbf{y_i}$ is a vector representing the observations for CE and SB respectively; $\mathbf{X_i}$, $\mathbf{Z}_{d\_i}$, $\mathbf{Z}_{m\_i}$ and $\mathbf{Z}_{hy\_i}$ are known incidence matrices for non-genetic, and direct and maternal genetic and herd-year effects, respectively; $\mathbf{b}_i$ is a vector of non-genetic effects, $\mathbf{a}_{d\_i}$ is a vector of the random direct additive-genetic effects of the calf (sire), $\mathbf{a}_{m\_i}$ is a vector of the random maternal additive-genetic effects of the dam (maternal grandsire), $\mathbf{h}_{hy\_i}$ is a vector of random herd-year effects and, **pe** is a vector of permanent environmental effects and **e** is a vector of residuals. Vectors $\mathbf{a}_{d\_i}$ and

$\mathbf{a}_{m\_i}$ were assumed to follow a multivariate normal distribution, with MVN(0, $\mathbf{G} = \mathbf{G_0} \otimes \mathbf{A}$) where, $\mathbf{G_0}$ was a 4 x 4 direct-maternal (S-MGS) variance-covariance matrix, $\otimes$ is the Kronecker product of matrices, and **A** was the relationship matrix.

Residuals, $\mathbf{e}_i$, and permanent environmental effects, $\mathbf{pe}_i$, were assumed to be MVN(0, $\mathbf{R}_e\,\sigma_e^2$), and MVN(0, $\mathbf{R}_{pe}\,\sigma_{pe}^2$), where $\mathbf{R}_e$ and $\mathbf{R}_{pe}$ denote the residual and permanent environmental 2 x 2 variance covariance matrices and σ_e^2 and σ_{pe}^2 were the residual variance and permanent environmental variance. Non-genetic effects in the model included sex of the calf, sex of the calf*parity interaction, year and month of calving, year*month of calving interaction; age of the dam (months)* parity interaction, and the interaction of herd*year of calving treated as a random factor. Table 2 shows the inbreeding coefficients of calves, dams and sires in the dataset which were calculated by RelaX2 (Strandén and Vuori, 2006), ranging from 0 to 0.298. All inbreeding coefficients were fitted in the bivariate model as fixed effects to evaluate their effect on the phenotype. Figure 1 shows the decreasing inbreeding rate and increasing effective population size (Ne) of the Murboden population in the last decade.

Table 2. Level of inbreeding for calves, dams and sires in the dataset (n=17,175)

Inbreeding coefficient (F)	Proportion of individuals		
	Calves	Dams	Sires
F = 0	21.37%	48.16%	52.13%
0 < F < 0.0625	76.25%	48.37%	46.13%
0.0625 ≤ F < 0.125	1.25%	2.06%	1.57%
0.125 ≤ F < 0.1875	0.56%	0.92%	0.16%
0.1875 ≤ F < 0.25	0.02%	0.03%	0
F ≥ 0.25	0.55%	0.45%	0.02%
Mean F ± STD	0.0126 ± 0.024	0.00941 ± 0.025	0.0051 ± 0.025
Min ; Max	0 ; 0.298	0 ; 0.289	0 ; 0.25

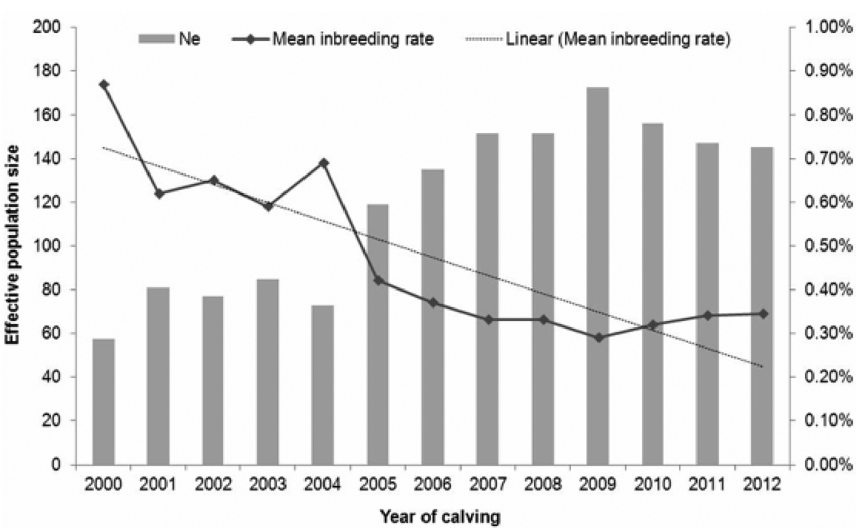

Figure 1.
Diagrammatic representation of the mean inbreeding rate and effective population size per year of calving

Results and discussion

Genetic parameters

Table 3 presents the estimated genetic parameters for CE and SB. The direct and maternal heritability of CE hence the heritability of 'ease of birth' and that of 'ease of calving' in the Murboden breed are both significantly different from 0 and are consistent with a well documented trend for CE heritabilities i.e. the maternal heritability is considerably lower than the direct heritability. Both estimated heritabilities are relatively high for the Murboden compared to for example the Holstein-Friesian breed (8% direct, 3% maternal, Eaglen et al., 2012). This is positive as genetic progress will be faster when the trait is selected upon. The heritabilities are however not out of range of estimates published in literature, especially for beef cattle (Ramirez-Valverde et al., 2001), which gives confidence in the analyses. The genetic direct-maternal correlation for CE is estimated at approximately -0.41±0.12. A negative direct-maternal genetic correlation is commonly found in CE and causes some concerns for selection. It primarily means that selection on solely the direct or maternal breeding value is discouraged as the total response to selection could be lower or even in the opposite direction as was intended (Eaglen et al., 2012). Instead, selection on a total breeding value i.e. direct+maternal is more sensible. Estimated parameters for SB are in the range of genetic parameters published in literature for this trait. Here, the maternal heritability *is* considerably smaller than the direct heritability, which is, again, a general trend shown for calving traits such as SB. Both heritabilities are however significantly different from zero. The direct heritability is on the higher side of the range generally reported for both dairy cattle breeds such as Holstein-Friesian, and beef breeds such as Hereford and Charolais despite the relatively moderate SB frequencies (Erikkson et al., 2004, Table 2). Genetic parameters estimated for the Austrian dual purpose breeds Fleckvieh and Brown Swiss show a direct heritability of 0.02 and a maternal heritability of 0.01 (Fuerst and Egger-Danner, 2003) The genetic covariance of stillbirth is notoriously difficult to estimate and values for the genetic correlation range from -1 to 1 in literature (Eaglen et al., 2012). This study is no exception showing a correlation of 0.83±0.25 that is not significantly different from 1 thus suggesting direct and maternal SB are the same trait. Genetic correlations between CE and SB show a strong postive genetic relationship between CE maternal and SB maternal (0.73±0.17), which would suggest that, genetically, an individual calving with more difficulty is genetically prone towards giving birth to a stillborn calf. The direct-direct genetic correlation between CE and SB is not significantly different from zero, which is contrary to most reports which support the hypothesis that a calf which is born more difficult is genetically prone to be stillborn. In the Murboden breed however, this relationship appears to be primarily phenotypic. A significant relationship was also detected between direct SB and maternal CE although this re-

Table 3. Estimated heritabilities (diagonal) and genetic correlations (off-diagonal) between calving ease (CE) and stillbirth (SB

	CEd	Cem	SBd	SBm
Calving Ease direct (CEd)	0.18 ± 0.04*			
Calving Ease maternal (CEm)	-0.41 ± 0.12*	0.11 ± 0.02*		
Stillbirth direct (SBd)	0.12 ± 0.17	0.49 ± 0.16*	0.05 ± 0.01*	
Stillbirth maternal (SBm)	-0.03 ± 0.22	0.73 ± 0.17*	0.83 ± 0.25*	0.02± 0.01*

* P<0.05

Table 4. Mean CE score per dam inbreeding category

Inbreeding Category	Mean Calving Ease Score±[2]
1. (F[1] = 0)	1.28 ± 0.046[a]
2. (0 < F < 0.0625)	1.32 ± 0.046[b]
3. (0.0625 ≤ F < 0.125)	1.39 ± 0.057[c]
4. (0.125 ≤ F < 0.1875)	1.47 ± 0.068[c]
5. (0.1875 ≤ F < 0.25)	1.41 ± 0.266
6. (F ≥ 0.25)	1.25 ± 0.126

[1] F=inbreeding coefficient; [2] Standard error of the mean; [a,b]= P<0.05.

lationship is notoriously difficult to interpret i.e. a stillborn calf by default will not become an adult cow.

Comparison of the results from this study with the parameters estimated by Manatrinon et al. (2009) demonstrates the importance of increasing datasets for the estimation of genetic parameters (in particular maternal variances and covariances) for calf performance traits given their relatively low heritabilities.

Inbreeding depression

Reduction of phenotypic performance due to inbreeding is termed inbreeding depression. In this study we have evaluated inbreeding depression in direct and maternal CE and SB. After having detected a significant effect of dam inbreeding on CE, fitted as a covariate (regression coeff: 0.75) we categorized the dam inbreeding coefficients into 6 categories following Table 2 and estimated mean CE score of inbreeding category by the PREDICT statement in ASREML. Table 4 shows a significant increase in CE score as inbreeding coefficients increase. 1% increase in dam inbreeding is associated with an increase of 0.55% in probability for a difficult calving. Or, individuals with an inbreeding coefficient between 6.25% and 12.5% show 5.5% more difficult calvings compared to non-inbred individuals. This percentage increases to 10.28% for individuals with inbreeding coefficients between 12.5% and 18.75%. Studies that attempt to quantify inbreeding depression on calving performance in beef cattle are rare and mainly limited to the Holstein-Friesian breed (McParland et al., 2007; Adamec et al., 1982). The effect found in this study on the Murboden is larger than reported for the Holstein-Friesian (McParland et al., 2007; Adamec et al., 1982) yet similar to the effect found in first parity Angus cattle (McParland et al., 2008). Dam inbreeding did not significantly affect SB, which is slightly surprising as inbreeding increases the risk of recessive deleterious alleles to be co-expressed which has a well reported effect on functional traits such as SB (Adamec et al., 1982; McParland et al., 2007, 2008). It is possible however, given the low heritabilities of SB, that simply more data is needed to detect an effect of inbreeding on SB in the Murboden breed. Calf inbreeding nor sire inbreeding had a significant effect on either trait. This is supported by literature on calf inbreeding effects on CE (McParland et al., 2007, 2008).

Conclusions

Calving performance in the Murboden is currently worrying. However, this study demonstrated that heritabilities of both calving ease and stillbirth are considerable. Hence, genetic progress will be relatively fast assuming the publication of estimated breeding values and the correct implementation of these. Dam inbreeding significantly affects calving ease and is likely to have been a contributor to the current high prevalence of difficult calvings. Implementation of mating advice programs that simultaneously restrict inbreeding rate and increase the genetic level of the next generation such as 'Optimum Contribution Selection' are thus likely to have a double positive effect on the reduction of calving problems within the Murboden breed.

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