Effect of inbreeding depression on survival of Austrian Brown Swiss calves and heifers

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ABSTRACT

The aim of this study was to estimate inbreeding depression for juvenile mortality in Austrian Brown Swiss replacement heifers born in the years 2001 to 2007. After data editing, records of 69,571 animals were investigated. In total, the pedigree consisted of 203,894 animals. Mean and median inbreeding coefficients were 0.0514 and 0.0475, respectively. The following periods were defined for analyses of juvenile mortality: P1 = 48 h to 30 d, P2 = 31 to 180 d, P3 = 181 to the day before first calving or a maximum age of 1,200 d if no calving was reported, P4 = 48 h to the day before age at first calving or a maximum age of 1,200 d if no calving was reported. Mortality during the first 30 d of life was 3.2%; in the total rearing period, 9.3% of the heifers died (excluding slaughtered and exported animals). For the estimation of the effect of inbreeding and of genetic parameters a linear animal model with the random effects herd-year of birth and animal as well as the fixed effects year of birth-month of birth and dam parity, and the continuous effect of inbreeding coefficient (linear and quadratic) was applied. The model was reduced to the linear effect of inbreeding as the quadratic term was not found to have a significant effect. Inbreeding significantly affected all traits unfavorably. In the full rearing period (P4), heifer calves with an inbreeding coefficient of 0.10 had a 4.9% higher mortality rate than heifer calves with no inbreeding.

Key words: Brown Swiss cattle, inbreeding depression, mortality, heifer

INTRODUCTION

Apart from stillbirth rate, survival of calves and heifers is among the less frequently studied functional traits

in dairy cattle. Many factors may influence mortality in young breeding stock. Among the most important ones are dystocia, respiratory diseases, and diarrhea; along with those, various environmental and physiological factors (e.g., Svensson et al., 2006; Lombard et al., 2007; Gulliksen et al., 2009) but also genetics (e.g., Fuerst-Waltl and Fuerst, 2010; Fuerst-Waltl and Sørensen, 2010; Henderson et al., 2011) were found to affect survivability. Another internal factor possibly having an effect on calf and heifer mortality is inbreeding. The inbreeding coefficient describes the probability that 2 alleles are identical by descent. The decrease in performance due to inbreeding is known as inbreeding depression (Falconer and Mackay, 1996). Inbreeding depression may be explained by different hypotheses. As reviewed by Wright et al. (2008), the partial dominance theory is generally considered to be the main reason for inbreeding depression but evidence for the overdominance hypothesis also exists. The partial dominance hypothesis reflects the fact that by inbreeding the frequency of homozygotes is increased and, thus, deleterious recessive alleles have a higher probability of being expressed. The overdominance hypothesis is based on the assumption that heterozygotes are superior to either homozygote. Inbreeding thus reduces the proportion of superior heterozygotes. Further, inbreeding depression may be explained by the separation of epistatic interaction between loci (Templeton and Read, 1994). Generally, inbreeding depression is stronger in traits that are closely related to fitness (e.g., survival and fertility) than in other traits (DeRose and Roff, 1999). Inbreeding depression is well documented for many fitness-related traits in plants, animals, and humans (Charlesworth and Willis, 2009) including stillbirth (e.g., Adamec et al., 2006) and longevity (e.g., Sewalem et al., 2006) in dairy cattle. However, to our knowledge, no studies have been published on inbreeding depression for calf and heifer survival in dairy cattle. Hence, the objective of this study was to estimate inbreeding depression on the survival of replacement stock in Austrian Brown Swiss at different ages as well as conducting a genetic analysis for these traits.

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MATERIALS AND METHODS

Data

Records of Austrian Brown Swiss calves and heifers born between January 1, 2001, and December 31, 2007, were extracted from the nationwide cattle performance database. Information about survival of calves is available due to the obligatory cattle registration in the European Union [regulation (European Commission, EC) no. 1760/2000] and was obtained for the period between January 1, 2001, and February 10, 2008. Data were further restricted to singleton females, a maximum foreign gene proportion of 12.5%, as well as to animals with full records regarding calving ease, herd, and parentage. Animals slaughtered or exported during their first 30 d of life were discarded as well as animals that were sold to another farm. Furthermore, records of dams with a length of pregnancy less than 270 or greater than 306 d, and an age at first calving lower than 550 d or higher than 1,200 d were excluded in accordance with the routine breeding value estimation procedures. After that, data were restricted to herd-year of birth classes having a minimum of 5 records, and sires having at least 10 daughters.

In accordance to earlier studies in Austrian dual-purpose Fleckvieh (Fuerst-Waltl and Fuerst, 2010) and Danish Holstein (Fuerst-Waltl and Sørensen, 2010), survival was analyzed in different defined periods: **P1** = 48 h to 30 d (born dead and died by 48 h postpartum is defined as stillbirth; Fürst and Fürst-Waltl, 2006), **P2** = 31 to 180 d, **P3** = 181 d to the day before first calving or a maximum age of 1,200 d, and **P4** = from 48 h to the day before first calving or a maximum age of 1,200 d. Periods P1 and P2 correspond to neonatal and calf mortality as defined by Wathes et al. (2008). According to the suggestion of Fuerst-Waltl and Fuerst (2010), only one period (P3) was defined for heifer mortality. Period P4 corresponds to the full period between birth and first calving, not including the day of calving itself. Thus, losses due to dystocia are not considered for the analysis of heifer mortality. Records of calves and heifers that were slaughtered or exported within a period and those too young to theoretically reach the maximum age of the respective period were set to missing for the period in question or subsequent periods, but their records were kept for preceding periods. The calves and heifers were scored as 1 if they died within the respective period and 0 otherwise.

In total, records of 69,571 calves and heifers of 933 sires were investigated. Pedigree information was also extracted from the national database and was traced back as far as possible to animals born in 1950 or

later. The pedigree consisted of 203,894 animals. Data preparation and descriptive statistics were carried out by software package SAS 9.2 (SAS Institute, 2008). Inbreeding coefficients were calculated with the program RelaX2 (Strandén and Vuori, 2006) using a modified algorithm based on the method of Meuwissen and Luo (1992). Using the same software, the complete generation equivalent (Maignel et al., 1996) was calculated to describe the quality of the pedigree. This measure is defined as the sum of the proportion of known ancestors over all generations traced.

Statistical Analysis

The software package ASReml (Gilmour et al., 2006) was used to estimate the effect of inbreeding on survival traits of calves and heifers. In an earlier genetic analysis of such traits in Austrian Fleckvieh (Fuerst-Waltl and Fuerst, 2010) and Danish Holstein (Fuerst-Waltl and Sørensen, 2010), threshold models accounting for the binary nature of the data were also applied and compared with linear models. In this study, the focus is on linear models as (1) the methodology (linear vs. threshold) was found to have little effect on the results in the above-mentioned studies and (2) the regression coefficients are on an interpretable scale when applying linear models. Thus, all traits were analyzed with univariate linear animal models:

$$Y_{ijkl} = \mu + HY_i + YM_j + Parity_k + b_1F + b_2F^2 \\ + animal_l + \varepsilon_{ijkl},$$

where Y_{ijkl} = individual observation of mortality in P1 to P4, μ = the overall mean, HY_i = the random effect of herd $\times$ year of birth (herd = 1, . . . , 154; year = 2001, . . . , 2007), YM_j = the fixed effect of year of birth $\times$ month of birth j , $Parity_k$ = the fixed effect of the dam's parity k ($k = 1, . . . , 5$, with parities >5 set to 5), b_1 and b_2 = regression coefficients, F = the continuous effect of the inbreeding coefficient (linear and quadratic), $animal_l$ = the random genetic effect of animal l , and ε_{ijkl} = the random residual. Further, 6 genetic groups were defined depending on country of origin.

Heritability was estimated as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{hy}^2 + \sigma_e^2},$$

with σ_a^2 , σ_{hy}^2 , and σ_e^2 being additive genetic, herd-year, and residual variances, respectively.

Table 1. Completeness of pedigree per generation in percent for studied animals per birth year (year) and across birth years (total)

Year	n	Completeness per generation (%)							
		1	2	3	4	5	6	7	8
2001	9,063	100.0	98.7	95.9	89.7	52.8	6.1	0.0	0.0
2002	9,664	100.0	98.6	96.4	90.3	59.2	9.3	0.0	0.0
2003	9,389	100.0	98.7	96.8	90.2	65.0	10.7	0.1	0.0
2004	9,498	100.0	98.7	97.1	92.1	66.0	14.0	0.0	0.0
2005	10,335	100.0	99.0	97.3	94.0	75.0	18.8	0.3	0.0
2006	10,982	100.0	98.8	97.5	93.7	75.7	20.5	0.1	0.0
2007	10,640	100.0	99.2	97.7	94.0	78.3	26.4	0.3	0.0
Total	69,571	100.0	98.8	97.0	92.1	68.0	15.5	0.1	0.0

RESULTS

Descriptive Statistics

The completeness of pedigree per generation is presented in Table 1. Complete pedigrees were available up to the seventh ancestor generation. The complete generation equivalent across birth years ranged from 9.00 (2001) to 10.07 (2007). In Table 2, the level of inbreeding is shown for the 69,571 Brown Swiss heifer calves under study. Only 511 animals were not inbred at all, 69 individuals had inbreeding coefficients equal to or higher than 0.25, with the maximum inbreeding coefficient being 0.33. Mean and median inbreeding coefficients were 0.0514 and 0.0475, respectively. From the birth years 2001 to 2007, a steady increase of the mean inbreeding coefficient from 0.045 to 0.058 could be observed. Mean inbreeding coefficients for the total population were slightly lower than those of the studied animals (Figure 1).

During the first month of life, the mortality of the analyzed 69,571 Brown Swiss heifer calves was 3.2% (Table 3). Of all heifer calves dying within P1 in this study, 50% died within the first 12 d. In later periods P2 and P3, mortality rates were lower. Of the 35,299 heifers theoretically reaching the maximum age of 1,200 d at the end of the total period between birth and age of first calving (P4), 21.6% were slaughtered or exported and 7.3% died; the median age of death was 59 d. When excluding slaughtered and exported

animals, the mortality accounts for 9.3% in P4. Large phenotypic differences were found for the offspring of different sires. For the 277 bulls with a minimum of 50 recorded heifers in the data set, mortality rates in P1 ranged from 0 to 10.4%. The corresponding range for the full period P4 and 113 bulls was 0 to 20%.

Inbreeding Depression

The results for all effects in the model including the solution for the inbreeding coefficient are shown in Table 4. The model was reduced to the linear effect of inbreeding for all periods under study, as the quadratic term was not found to have a significant effect. In the reduced model, inbreeding significantly affected all traits unfavorably with $P < 0.001$ for P1, P2, and P4 and $P < 0.01$ for P3, respectively. For heifers with inbreeding coefficients of 0.10, the average mortality was 1.8, 1.2, 1.5, and 4.9% higher for P1, P2, P3, and P4, respectively, than for noninbred heifers. All other effects were highly significant for P1 only; dam parity additionally had a significant effect for P4, whereas a trend could be observed for P2. Generally, mortality of offspring of dams in earlier lactations was higher.

Genetic Parameters

Estimated variance components and heritabilities are presented in Table 5. Heritabilities for P1, P2, and P3 and the linear animal model were lower than 0.01, ranging from 0.002 (P3) to 0.009 (P1). For P4, a value ($\pm$ SE) of 0.014 ± 0.005 was estimated.

Table 2. Level of inbreeding (F = inbreeding coefficient) for the studied heifer calves (n = 69,571)

Inbreeding coefficient	Proportion of individuals (%)
$F = 0$	0.73
$0 < F < 0.0625$	75.05
$0.0625 \leq F < 0.125$	23.09
$0.125 \leq F < 0.1875$	0.96
$0.1875 \leq F < 0.25$	0.07
$F \geq 0.25$	0.10

DISCUSSION

The quality of the pedigree is a very important factor when interpreting inbreeding coefficients. With a complete generation equivalent between 9.0 and 10.1 and a completeness of the pedigree for the fourth ancestor generation ranging from 89.7 to 94.0% (Table 1) for the

Table 3. Number of observations in total (n); number of animals that died, were culled, or were exported in different periods (P1 = 2–30 d, P2 = 31–180 d, P3 = 181 d to day before first calving or a maximum of 1,200 d, and P4 = 2 d to day before first calving or a maximum of 1,200 d); and median age at death

Period	n ¹	Animals slaughtered or exported	Animals died	Median age at death (d)
P1	69,571	— ²	2,200	12
P2	62,372	1,768	1,408	68
P3	32,326	6,391	842	454
P4	35,299	7,626	2,580	59

¹Excluding animals not (theoretically) reaching the maximum age of period.

²Due to data editing, 405 animals being exported or slaughtered during the first 30 d of life were excluded from analysis.

birth years 2001 and 2007, respectively, the depth and quality of the available pedigree may be considered as rather high. The mean inbreeding coefficient of Austrian Brown Swiss in the birth year 2001 was 0.045 and is comparable to that in the American Brown Swiss population (Weigel, 2001). The mean inbreeding coefficients for the studied animals born in the years 2001 to 2007 were almost identical to those for the same birth years in the total population (Figure 1). The rather strong editing process, thus, did not affect the level of inbreeding in this study. Similar to other dairy cattle populations, an increase in inbreeding could be observed during the last centuries (e.g., Sørensen et al., 2005; Sewalem et al., 2006; McParland et al., 2007a).

The mortality of heifers during the first month of life reported in the present study (3.2%) was higher than that in Austrian Fleckvieh cattle (1.8%, Fuerst-Waltl and Fuerst, 2010), but in accordance to values reported in other countries and breeds (e.g., 3.4 and 3.2% in British cattle; Brickell et al., 2007) and Danish Holstein cattle (Fuerst-Waltl and Sørensen, 2010), respectively. In an older study in US Brown Swiss heifer calves (Erf et al., 1990), a mortality of 2.6% was reported for the first week of life. Differences in the definition of stillbirth, however, have to be taken into account when interpreting early postnatal mortality. Whereas in many countries, stillbirth is defined

as being born dead or died within 24 h after birth, in the joint Austrian-German genetic evaluation, calf mortality up to 48 h contributes to stillbirth (Fürst and Fürst-Waltl, 2006). Nevertheless, the stillbirth rate of 4.3%, as published in the previously cited investigation for Austrian Brown Swiss in 2005, is lower than in most other dairy cattle populations. For example, in Danish Holstein cattle, a stillbirth rate of 9.5% for first and 5.4% for later calvings was reported in the year 2008 (Team Avlsværdiurdering Dansk Kvæg, 2009). Similar stillbirth rates were, for example, shown for Canadian and US Holsteins (Meyer et al., 2001; Van Doormaal and Brand, 2006).

In accordance with studies on Austrian Fleckvieh (Fuerst-Waltl and Fuerst, 2010) and Danish Holstein (Fuerst-Waltl and Sørensen, 2010), more animals died during the first month of life than between 1 and 6 mo. This confirms that also in Brown Swiss, the risk of calf mortality is highest during the early stages of life. In Danish Jersey heifers (Norberg, 2008), mortality was analyzed during the first 180 d of life. A rather alarming proportion of 12.5% of all heifer calves died during the first half year after birth.

For the full period until first calving and excluding slaughtered or exported animals from analysis, the mortality of Austrian Brown Swiss heifers (9.3%) was also higher than that of Austrian Fleckvieh heifers (5.6%;

Table 4. Levels of significance (*P*-value) for effects in the model as well as solutions (SE in parentheses) for regression coefficients in different periods¹

Effect	P1 (n = 69,571)	P2 (n = 60,604 ²)	P3 (n = 25,935 ²)	P4 (n = 27,673 ²)
Levels of significance (<i>P</i> -value)				
Year × month	<0.001	NS ³	NS	NS
Dam parity	<0.001	0.081	NS	<0.001
Inbreeding coefficient (linear)	<0.001	<0.001	0.011	<0.001
Regression coefficient				
Inbreeding coefficient – linear	0.176 (0.036)	0.115 (0.033)	0.151 (0.059)	0.495 (0.097)

¹Models were reduced to linear regression coefficients, as the quadratic term was not significant for any period. Periods: P1 = 2–30 d, P2 = 31–180 d, P3 = 181 d to day before first calving or a maximum of 1,200 d, and P4 = 2 d to day before first calving or a maximum of 1,200 d.

²Animals exported or slaughtered were set to missing.

³NS: *P* > 0.10.

Figure 1. Mean inbreeding coefficient in the Austrian Brown Swiss population (females only, solid line) and in the studied animals (dashed line).

Fuerst-Waltl and Fuerst, 2010) but comparable with Danish Holsteins (9.4%; Fuerst-Waltl and Sørensen, 2010). For British dairy farms, Wathes et al. (2008) reported a juvenile mortality rate (i.e., the mortality between 6 mo of age and the start of the service period at about 15 mo) of 3.5%. However, the authors merged dying and culling events into one single category.

In this analysis, mortality in all stages of replacement heifers' lives was unfavorably affected by inbreeding. Given that overall mortality in the rearing period accounts for 9.3% (excluding slaughtered and exported heifers), the increase of 0.49% mortality per 1% in-

breeding may be interpreted as being rather high. Standardized estimates make the extent of inbreeding depression all the more evident. Expressed as percentages of genetic standard deviations, inbreeding depression per 1% inbreeding is as large as 10.4, 11.5, 22.5, and 14.3% for P1, P2, P3, and P4, respectively. McParland et al. (2007b) observed considerably lower inbreeding depression for the functional traits age at first calving, calving interval, and survival of cows. For these traits, standardized estimates of inbreeding depression ranged from 1.2 to 1.6% only. However, with corresponding values of 15.6 to 21.9% of the additive genetic standard

Table 5. Variance (σ^2) components (a = additive genetic, hy = herd-year, e = residual) and heritabilities (h^2) $\pm$ SE estimated for calf and heifer mortality in different periods

Period ¹	Variance component			
	σ_a^2	σ_{hy}^2	σ_e^2	h^2
P1	0.0003	0.0007	0.0295	0.009 $\pm$ 0.002
P2	0.0001	0.0004	0.0222	0.005 $\pm$ 0.002
P3	<0.0001	0.0012	0.0301	0.002 $\pm$ 0.003
P4	0.0012	0.0044	0.0787	0.014 $\pm$ 0.005

¹Periods: P1 = 2–30 d, P2 = 31–180 d, P3 = 181 d to day before first calving or a maximum of 1,200 d, and P4 = 2 d to day before first calving or a maximum of 1,200 d.

deviation for milk concentration traits, the authors reported higher inbreeding depression for traits related to milk production. When interpreting the results of inbreeding depression in P2 and P3, preselection of data also needs to be considered. Analysis of mortality in these periods is conditional on the calves and heifers surviving the previous periods. In this context, the rather low inbreeding depression for functional traits in the study of McParland et al. (2007b) may also partly be explained. Both, fertility and survival of cows during their first lactation may only be analyzed in animals that conceived as heifers and survived to first calving.

To our knowledge, this is the first study analyzing inbreeding effects on juvenile mortality in dairy cattle. However, in other species, evidence for inbreeding depression on juvenile mortality was found (e.g., Ralls and Ballou, 1982; Köck et al., 2009). In dairy cattle, inbreeding depression was reported for functional traits such as longevity of cows, male and female fertility, dystocia, stillbirth, SCC, and mastitis (e.g., Adamec et al., 2006; Sørensen et al., 2006; Maximini et al., 2011). Regarding the survival of cows, increased inbreeding in Austrian Brown Swiss (Fuerst and Sölkner, 1994) resulted in a decreased length of productive life. On average, the cows' length of productive life was decreased by 4.3 d per 1% increase in inbreeding. Similarly, in Canadian Jersey, Holstein, and Ayrshire cows, the relative risk of culling was significantly increased by inbreeding (Sewalem et al., 2006).

Calculated heritabilities were in the range of previously reported values for Austrian Fleckvieh cattle (<0.01 to 0.016 ; Fuerst-Waltl and Fuerst, 2010). Additional results for threshold logit sire models (data not shown) were also in accordance with heritabilities estimated for Austrian Fleckvieh cattle on the underlying scale (Fuerst-Waltl and Fuerst, 2010). In Danish Holstein heifers, slightly higher heritabilities were estimated for mortality in P1, P2, and in the full period (0.017 to 0.042 with a linear sire model; Fuerst-Waltl and Sørensen, 2010). Even though both mortality and involuntary culling contribute to rearing losses, they are most likely affected by different genes. Especially in heifers that have already been inseminated, poor fertility is expected to be among the main reasons for culling. However, disposal codes are not available for heifers. Hence, the categories died and slaughtered were not merged for this analysis. According to an earlier study in Austrian Fleckvieh cattle (Fuerst-Waltl and Fuerst, 2010), additional calculations were carried out for involuntary culling (data not shown). Involuntary culling of heifers was defined as animals that were slaughtered and having at least 1 insemination after 365 d and before 1,200 d. More than 2,000 animals fell into this category. With heritability (h^2) = 0.07 ± 0.01 ,

the estimated heritability was higher than in Fleckvieh ($h^2 = 0.02$). No significant inbreeding depression was found for this trait, though (1.4% more involuntary culling for heifers with an inbreeding coefficient of 0.10 compared with noninbred heifers, $P = 0.16$).

As suggested by Eaglen et al. (2011), the effects associated with difficult calvings may have long-term consequences on calves. In earlier genetic analyses of heifer mortality in Danish Holstein (Fuerst-Waltl and Sørensen, 2010) and Austrian Fleckvieh (Fuerst-Waltl and Fuerst, 2010) cattle, calving ease was also included in the model as a fixed effect. It was found to affect mortality in the early and full rearing period. However, although the inclusion of calving ease helps to explain mortality, the adjustment for calving ease may bias the genetic and the residual variances downwards (Fuerst-Waltl and Sørensen, 2010) and also have an effect on the estimate of inbreeding depression. In additional analyses (data not shown), the models were also run including calving ease as a fixed effect. In Austrian Brown Swiss, more difficult calvings significantly affected the mortality in P1 only; the estimates for heritability and inbreeding depression were almost identical when applying both models, with and without calving ease as fixed effect.

As calf and heifer mortality are economically very important traits in dairy cattle breeding (e.g., Østerås et al., 2007), they should be considered in breeding programs. Genetically improving calf and heifer mortality is feasible if genetic and phenotypic variations are reasonably high even if it is a so-called low-heritability trait. The value of potential additional information from a genetic evaluation for survival in the rearing period will also depend on the economic values for the traits. A similar functional trait, stillbirth, is being routinely evaluated in most developed countries. Even though in the case of stillbirth, 2 animals (the dam and the calf) are affected, it is likely that the economic value for mortality of heifers in the rearing period is higher than that for stillbirth. Given that the economic value in the total merit index is reasonably high, genetic gain may be achieved or at least a deterioration of the trait may be avoided. In future breeding program scenarios, genomic selection may also provide a chance for genetic progress in lowly heritable functional traits.

CONCLUSIONS

Inbreeding significantly affects juvenile mortality in Austrian Brown Swiss cattle and, thus, adds to a large number of functional traits in dairy cattle for which inbreeding depression has been reported. Apart from ethical issues concerning animal health and welfare, higher female calf or heifer mortality has negative ef-

fects on dairy farmers' profitability due to higher rearing costs and reduced possibility for selection. Both the genetic improvement of this trait and keeping inbreeding as low as possible are, thus, desirable. A mating planner for all cattle breeders with internet access was recently provided by the Federation of Austrian Cattle Breeders (Rinderzucht Austria, 2012). By means of this online application, the expected inbreeding of a potential offspring is calculated and, thus, close inbreeding can be easily avoided.

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