Udder Health Shows Inbreeding Depression in Danish Holsteins

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ABSTRACT

The purpose of this study was to estimate inbreeding depression for udder health using records on mastitis incidence and somatic cell count (SCC). Data were selected based on a pedigree completeness index so that inbreeding coefficients were reliable. Average inbreeding was 3.3%. The presence or absence of mastitis was considered in first (CM1), second (CM2), and third (CM3) lactations, and was recorded as a binary trait. Somatic cell count was also included and analyzed on the log scale. A minimum of 140,000 cows with records were included per trait. Linear sire models were used and (co)variance components were estimated. Linear and curvilinear effects of the coefficient of inbreeding were included. Inbreeding significantly affected all traits investigated. Three traits, CM1, CM3, and SCC, showed a nonlinear relationship between phenotype and inbreeding coefficient. A cow with 5% inbreeding compared with a cow with 2% inbreeding had a higher SCC and a higher incidence of mastitis. The SCC increased by 1,500 cells/mL in first lactation and the incidence of mastitis increased by 1.08, 0.55, and 0.98% in first, second, and third lactation, respectively. The corresponding reduction in net return from these traits over 3 lactations amounted to US\$11.00 under Danish production circumstances. These results are a step on the way to estimating the total cost of inbreeding depression to determine an acceptable rate of inbreeding. **Key words:** inbreeding depression, udder health, mastitis, somatic cell count

INTRODUCTION

The focus of dairy cattle breeding has shifted during the last few decades from almost exclusive attention on production traits to the incorporation of cost-reducing functional traits in the breeding goal. Besides having low heritabilities, these functional traits are also expected to be prone to inbreeding depression. Significant inbreeding depression for milk, fat, and protein produc-

tion has been found in a number of populations including North American Holsteins (e.g., Miglior et al., 1995b), North American Jerseys (e.g., Miglior et al., 1992), and Swiss Braunvieh (Casanova et al., 1992). Inbreeding depression has been estimated for some functional traits in dairy cattle (Smith et al., 1998; Thompson et al., 2000a,b; Adamec et al., 2006). Inbred animals tend to be older at first calving, have longer calving intervals, have fewer days of productive life, and have a higher risk of giving birth to stillborn calves.

DeRose and Roff (1999) reviewed studies on inbreeding depression in 54 species of wild and laboratory populations. They concluded that life history traits, such as fertility, fecundity, and survival, exhibited approximately 6 times as much inbreeding depression as conformation traits, such as adult body size. Inbreeding has been shown to reduce resistance to infectious diseases in other species in the laboratory (e.g., Spielman et al., 2004) and in the wild (e.g., Acevedo-Whitehouse et al., 2003). Inbreeding depression comparisons of livestock and wild or laboratory populations are not straightforward because selection pressure and rates of inbreeding can and will be different. However, it does not compromise the general conclusion of DeRose and Roff (1999) that life history traits are more prone to inbreeding depression than conformation traits. Milk production traits can be considered life history traits in the evolution of cattle because they contribute to offspring survival and therefore would be expected to show significant inbreeding depression, as has been seen.

To date, no studies have been published on inbreeding depression for mastitis incidence in dairy cows. However, some studies have estimated inbreeding depression for SCC. Miglior et al. (1995a) estimated a linear inbreeding depression in SCS to be 10.5% of a phenotypic standard deviation for a change of 0.1 in the inbreeding coefficient. Smith et al. (1998) and Thompson et al. (2000a,b) also estimated inbreeding depression for SCS but found no significant results. The Nordic countries, including Denmark, have a thorough system for gathering registrations on veterinary treatments, including mastitis treatments (Bundgaard and Høj, 2000). Therefore, these data can be used to test for the presence of inbreeding depression for udder health.

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Table 1. Phenotypic means and number of records, herds, herd-year-season (HYS) groups, sires, and animals in the pedigree file for the 4 traits

Trait ¹	Mean	No. records	No. herds	No. HYS	No. sires	Size of pedigree file
CM1	26.1%	376,363	8,256	38,305	3,271	19,156
CM2	28.0%	340,044	11,012	65,963	4,672	19,156
CM3	32.4%	144,222	9,452	43,723	2,805	19,156
SCS	11.26	529,377	9,703	53,060	4,068	15,654

¹Incidence of mastitis in first (CM1), second (CM2), or third (CM3) lactation. Average SCC in first lactation was transformed to SCS using the natural logarithm prior to analysis. The mean SCC was 77,700 cells/mL, with 67% of the observations being between 36,600 and 164,900 and 95% of the observations being between 17,200 and 350,100.

A recent investigation has shown that inbreeding has accumulated rapidly (approximately 1% per generation) in Danish Holsteins over the last decade (Sørensen et al., 2005). Therefore, this breed is expected to show inbreeding depression for functional traits such as mastitis incidence and SCC. This paper tests the hypothesis that inbreeding increases the incidence of mastitis in the first 3 lactations and the SCS in the first lactation of dairy cows.

MATERIALS AND METHODS

Data

The Danish Cattle Database (Bundgaard and Høj, 2000) provided records of mastitis treatments and SCC for this study. Incidence of mastitis in first (CM1), second (CM2), and third (CM3) lactation and the average SCC in first lactation were analyzed. The traits considered in this study are used in the routine genetic evaluation and are therefore stored as described below. The period from 10 d preceding calving to 305 d after calving in first lactation was covered by CM1, whereas CM2 and CM3 covered the period from 10 d preceding calving to 100 d after calving in the second and third lactations, respectively. Mastitis incidence was recorded as a binary trait; either the cow was treated for mastitis (one or more times) during the period (in which case it was coded as 1) or it was not treated (in which case it was coded as 0). Somatic cell count was transformed to SCS using the natural logarithm prior to analysis. Table 1 summarizes the data used in this study.

We used the data set from the routine genetic evaluation, with additional editing according to the pedigree completeness. The degree of completeness of pedigrees was assessed for each cow individually by the index proposed by MacCluer et al. (1983). The coefficient for pedigree completeness (PEC), to quantify the possibility for detecting inbreeding in the pedigree, was

$$PEC_{animal} = \frac{2C_{sire}C_{dam}}{C_{sire} + C_{dam}},$$

where C_{sire} and C_{dam} are contributions from the paternal and maternal lines respectively, and

$$C = \frac{1}{d} \sum_{i=1}^d a_i,$$

where a_i is the proportion of known ancestors in generation i , and d is the number of generations taken into account. In this study, 5 generations are considered when calculating this index for each animal ($d = 5$). Records were included only if the cow had a pedigree completeness index of at least 0.9. This is comparable to the situation when one great-grandparent is unknown or when 2 great-great-grandparents are unknown. Individual inbreeding coefficients were calculated using the algorithm by Meuwissen and Luo (1992) and all available pedigree information. The average inbreeding was 3.3%, and the distribution of inbreeding coefficients of animals born in 2002 with a pedigree completeness of at least 0.9 shown in Figure 1 illustrates the overall distribution of inbreeding.

After having selected the animals with adequate pedigree completeness, additional editing was performed to have a minimum of 5 records per herd-year-season group and at least 20 daughters per sire for traits CM1 and SCS. For CM2 and CM3 a minimum of 3 records per herd-year-season group and at least 10 daughters per sire were required. This editing was done to use the most informative observations, given computational constraints. After the editing for pedigree completeness and size of herd-year-season groups and daughter groups, approximately one-third of the total records were left in the data set.

Models

The sire models used in the Danish routine genetic evaluation (Danish Agricultural Advisory Centre, 2003)

Figure 1. Distribution of inbreeding coefficients of animals born in 2002 with a pedigree completeness of at least 0.9.

were used, with the addition of linear and quadratic regressions on the coefficient of inbreeding to the fixed part of the model. The model used is as follows:

$$Y_{ijk(l)m} = HYS_j + MY_k + AC_l + b_1F_i + b_2F_i^2 + s_m + e_{ijk(l)mi}$$

where $Y_{ijk(l)m}$ is the observation of CM1, CM2, CM3, or SCS for cow i ; HYS_j is the fixed effect of the j th herd-year-season of the observation group; MY_k is the fixed effect of the k th month-year of the calving group; AC_l is the fixed effect of the l th age of the calving group (for CM1 and SCS only); b_1F_i is the regression on the coefficient of inbreeding for cow i ; $b_2F_i^2$ is the regression on the squared coefficient of inbreeding for cow i ; s_m is the random effect of sire m for cow i ; and $e_{ijk(l)mi}$ is the random residual of the observation for cow i . The traits CM1, CM2, and CM3 were analyzed in a trivariate model. This model allowed for selection from earlier to later lactations as well as for environmental and genetic correlations of observations.

The pedigrees of sires were traced in an animal model fashion as far back as possible. The models were analyzed using the program DMU (Madsen and Jensen, 2000), which uses an implementation of the AI-REML algorithm (Jensen et al., 1997) for estimating (co)variance components. The inverse of the relationship matrix of sires was set up, taking inbreeding into account. Because (co)variance components are estimated simultaneously, the estimates of regression coefficients are not the best linear unbiased estimates, but rather empirical best linear unbiased estimates.

We used linear models for the analysis, despite the binary character of the data, for 2 reasons. First, a simulation study by Mäntysaari et al. (1991) showed no significant improvement in estimation of (co)variance components by using a threshold model over a linear model as long as the incidence is at least 25% and at

most 75%. All mastitis traits considered in this study fall in this interval. Second, analysis of data on the observed scale allows straightforward interpretation of the estimates of inbreeding depression.

RESULTS

Inbreeding significantly affected all 4 traits unfavorably (Table 2). For 3 traits (CM1, CM3, and SCS) the quadratic regression was significantly negative, indicating that the cost of an extra percentage unit of inbreeding is lower at higher levels of inbreeding (e.g., 0.10) than at lower levels (e.g., 0). However, the predicted incidence of mastitis increased in the entire interval of inbreeding coefficients between 0 and 0.1 (Figure 2). The predicted level of SCC also increased continuously in the same interval.

Coefficients of inbreeding of 2 and 5% are comfortably within the distribution of inbreeding coefficients (Figure 1). This allows for robust comparison of inbreeding depression at representative values of inbreeding. Cows with an inbreeding coefficient of 0.05 were predicted to have 0.5 to 1.1% higher mastitis incidence compared with cows with an inbreeding coefficient of 0.02 (Table 2). Depending on lactation number, this represents 2 to 4% of the mean incidence. Under Danish production circumstances, this translates into a difference in economic net return of −1.90 to −3.80 €, corresponding to US\$−2.30 to −4.50, because an incidence of mastitis costs 348.00 € (Østergaard et al., 2005). For cows with 3 lactations, the difference is 9.10 € or US\$11.00 over their lifetime.

Estimates of variance components and heritabilities are presented in Table 3. Heritability estimates were similar to estimates from other studies in which the heritability for SCS ranged from 0.11 to 0.18 (Lund et al., 1999; Van Tassell et al., 2000; Ødegård et al., 2003), and the heritabilities for the mastitis traits ranged from 0.025 to 0.052 (Nielsen et al., 1999; Hansen et al., 2002; Lassen et al., 2003). Our heritability estimates were also very similar to the parameters used in the Danish routine genetic evaluation in a model excluding the effect of inbreeding on both the mean and the genetic covariance structure (Danish Agricultural Advisory Centre, 2003).

DISCUSSION

Here we studied inbreeding depression for 4 indicator traits of resistance to mastitis. All traits were significantly and unfavorably affected by inbreeding. This is the first report on inbreeding depression for mastitis incidence of which we are aware.

Inbreeding depression for SCC has been estimated in other studies. Differences between the results of this

Table 2. Estimates of significant ($P < 0.05$) linear and quadratic regressions on inbreeding¹ and predicted differences in mastitis incidence and SCC between cows with inbreeding coefficients of 0.05 and 0.02²

Trait ³	Regression		Difference				
	Linear	Quadratic	Absolute	Economic	Percentage of σ_P	Percentage of σ_A	Percentage of the mean
CM1	0.46 (0.08)	-1.51 (0.5)	1.08%	-3.80 €	2.6	11.8	4.1
CM2	0.18 (0.05)	NS	0.55%	-1.90 €	1.3	6.5	2.0
CM3	0.48 (0.1)	-2.27 (1.0)	0.98%	-3.40 €	2.2	10.6	3.0
SCS	0.84 ⁴ (0.1)	-2.53 ⁴ (0.7)	1,500 cells per mL ⁵		2.7 ⁴	7.0 ⁴	2.0 ⁵

¹Standard errors in parentheses. NS = not significant.

²Predicted differences are expressed in actual and economic units, and also as percentages of phenotypic (σ_P) and genetic (σ_A) standard deviations, and the mean of each trait.

³Incidence of mastitis in first (CM1), second (CM2), or third (CM3) lactation. Average SCC in first lactation was transformed to SCS using the natural logarithm prior to analysis.

⁴On the transformed scale.

⁵On the observed scale.

study and earlier studies are fairly small. Nonetheless, they can be explained by a number of factors differing between the studies. Smith et al. (1998) and Thompson et al. (2000a,b) considered multiple lactations and found no significant inbreeding depression. Van Tassell et al. (2000) also considered multiple lactations and found lower inbreeding depression (the regression estimate was 0.0037 per 0.01 increase in inbreeding) than in this study. This indicates that inbreeding depression is larger earlier in life. Miglior et al. (1995a) found a slightly higher estimate in Canadian Holsteins (3.2% of a phenotypic standard deviation per 0.03 increase in inbreeding; the regression estimate was 0.012 per 0.01 increase in inbreeding), and Mrode et al. (2004) found a slightly lower estimate in UK Holsteins (1.8% of a phenotypic standard deviation per 0.03 inbreeding; the regression estimate was 0.0039 per 0.01 increase in inbreeding). These 2 studies considered only first-lactation records of SCC, as in the present study. In both cases, the average level of inbreeding was lower than

in the present study (0.017 and 0.01, respectively). Because the effect of inbreeding on SCC in the present study was found to be nonlinear, the estimated inbreeding depression will depend on the mean and dispersion of inbreeding coefficients. In addition, the genetic background can be expected to influence the amount of inbreeding depression. The populations studied here and by Mrode et al. (2004) are undergoing upgrading to North American Holsteins, whereas the population studied by Miglior et al. (1995a) was more homogeneous. These different genetic backgrounds can influence the estimates of inbreeding depression.

The negative regression on the squared coefficient of inbreeding found in this study could be explained by many opportunities for selection on traits showing inbreeding depression, such as stillbirths (Adamec et al., 2006) and early fertility (Smith et al., 1998). If such selection is present, the cows with a high expected coefficient of inbreeding might have a smaller realized level of inbreeding on the genomic level. This kind of selection bias is not accounted for when only pedigree data are used to estimate the inbreeding coefficient. Analyses with animals grouped according to similar inbreeding coefficients allowed for estimation of the effect of in-

Figure 2. Predicted relationship between inbreeding coefficient and incidence of mastitis for first (thin line), second (intermediate line), and third (bold line) lactation.**Table 3.** Estimates of genetic (σ_A), environmental (σ_E), and phenotypic (σ_P) standard deviations for the 4 traits¹

Trait ²	σ_A	σ_E	σ_P	h^2
CM1	0.091	0.41	0.42	0.047 (0.004)
CM2	0.084	0.42	0.43	0.038 (0.003)
CM3	0.092	0.44	0.45	0.042 (0.005)
SCS	0.28	0.67	0.73	0.15 (0.006)

¹Estimates of heritability (h^2) are given with standard errors in parentheses.

²Incidence of mastitis in first (CM1), second (CM2), or third (CM3) lactation. Average SCC in first lactation was transformed to SCS using the natural logarithm prior to analysis.

breeding common to these groups as fixed class effects. A plot of these estimates gives essentially the same profile as in Figure 2 (results not shown). This means that the curvature is not an artifact of the regression approach. The presentation of the results of the studies by Thompson et al. (2000a,b) seemingly indicates the kind of curvature opposite the results presented in the present study. However, the points on the x -axis in those studies are not equidistant, thus disturbing the overall relationship.

The cost of a mastitis case is very sensitive to the incidence rate, herd management, quotas, and prices for milk and veterinary treatment (Seegers et al., 2003). Therefore, the cost of inbreeding depression for mastitis incidence presented in this paper is included only as an indication of the economic impact of inbreeding depression. Because the mastitis traits used in this study include only part of the total incidence of mastitis, the cost of inbreeding depression because of mastitis is likely to be underestimated. The \$11.00 difference in lifetime net return because of inbreeding depression for mastitis incidence between cows with inbreeding coefficients of 0.02 and 0.05 is smaller than the \$65.00 and \$73.00 differences in lifetime net return found by Smith et al. (1998) for registered US Holsteins in manufacturing and fluid markets, respectively. These last figures include the cost of inbreeding depression for fertility, production, and longevity, and are therefore larger than the cost for mastitis alone found in this study.

The amount of available pedigree information highly affects the credibility of the inbreeding coefficients. Two sources of error may occur. The first is that some ancestors are unknown. In that case, the unknown ancestor is assumed to be unrelated to the rest of the ancestors. This biases the calculated inbreeding coefficient downward. This bias has been partly avoided in this study by editing the data set to include only animals with high pedigree completeness. The second source of error is that some ancestors may have been recorded incorrectly. This adds noise to the calculated inbreeding coefficient. In Danish Holsteins the proportion of errors in the pedigree is 3.8%, according to a study of 266 calves and their parents (Nielsen and Nielsen, 2002). This number is smaller than has been found in similar studies in other countries. Visscher et al. (2002) found 10% errors in the UK dairy population, and Spelman (2002) refers to a study that found 12 to 15% errors in a New Zealand population.

Data were edited to avoid bias from incomplete pedigrees. This and the following editing to allow for a minimum of records per herd-year-season groups and daughter groups resulted in two-thirds of the records being discarded. This is a very high proportion and

could introduce other bias. Because younger animals tend to have more complete pedigrees, the editing resulted in an overrepresentation of young animals. However, this is not likely to cause any bias in the estimated inbreeding depression. It only makes the estimates more relevant as predictions of the cost of inbreeding in future generations.

Results from linear model analyses of binary data have been proved to be robust when estimating (co)variance components and ranking animals for selection (Mäntysaari et al., 1991). Whether linear models are equally robust in estimating inbreeding depression for binary traits has not been assessed in this study and remains open to discussion.

Because inbreeding significantly affects the phenotype of cows for mastitis incidence and SCC, the coefficient of inbreeding should be included in the fixed part of models for prediction of breeding values. Theoretically, if inbreeding is corrected for, the prediction of breeding values would be improved. Instead of penalizing animals that are heavily related to the rest of the population (i.e., have highly inbred daughters) by disregarding inbreeding in the prediction of breeding values, the better approach is to calculate the best possible predicted breeding values correcting for inbreeding depression, and then use an optimal contribution selection methodology (Meuwissen and Sonesson, 1998) that allows for an optimal weighting of genetic merit and relationship. The data set used in this study has been edited according to pedigree completeness, which will not be possible when predicting breeding values. However, VanRaden (1992) developed an algorithm in which animals with low pedigree completeness were assigned inbreeding coefficients according to the mean relationship of known ancestors of the same period. This makes it possible to include the inbreeding coefficient for all animals in routine genetic evaluation.

CONCLUSIONS

Inbreeding significantly affects the resistance of dairy cows to mastitis, as indicated by an increased incidence of mastitis in the first 3 lactations and an increase in SCC in the first lactation. Because mastitis is a costly disease in dairy production, inbreeding affects the economic return. This provides an incentive for controlling the rate of inbreeding in dairy populations.

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