

Inbreeding Effects on Milk Production, Calving Performance, Fertility, and Conformation in Irish Holstein-Friesians

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ABSTRACT

The objective of this study was to determine the effect of inbreeding on milk production, somatic cell count, fertility, survival, calving performance, and cow conformation in Irish Holstein-Friesian pluriparous dairy cows. Inbreeding was included in a linear mixed model as either a class variable or a continuous variable, where higher order polynomials of the latter were also tested in the model as an indicator of nonlinear inbreeding depression. The effects of dam inbreeding and calf inbreeding on calving-related traits were analyzed separately. Inbreeding had a deleterious effect on most of the traits analyzed, although inbreeding depression was sometimes nonlinear or differed significantly across parities. A primiparous animal, 12.5% inbred (i.e., following the mating of noninbred half-sibs), had milk, fat, and protein yields reduced by 61.8, 5.3, and 1.2 kg, respectively; fat and protein concentrations reduced by 0.05 and 0.01%, respectively; and somatic cell scores (i.e., natural log of somatic cell count divided by 1,000) increased by 0.03. The 12.5% inbred animal was also expected to have a 2% greater incidence of dystocia, a 1% greater incidence of stillbirth, a 0.7% greater incidence of male calves, an increase in calving interval of 8.8 d, an increase in age at first calving of 2.5 d, and a reduced survival to second lactation of 4 percentage units. Inbred animals were also taller, narrower, and more angular. Although the effects of inbreeding were statistically significant, they were small and are unlikely to cause great financial loss on Irish dairy farms. **Key words:** inbreeding depression, milk, dystocia, fertility

INTRODUCTION

Inbreeding is defined as the probability that 2 alleles at any locus are identical by descent (Falconer and

Mackay, 1996) and occurs when related individuals are mated to each other. The reduction in mean phenotypic performance associated with inbred animals is referred to as inbreeding depression (Falconer and Mackay, 1996) and can be of considerable economic loss to dairy producers (Smith et al., 1998; Croquet et al., 2006). Furthermore, inbreeding depression is generally greater in traits associated with fitness and survival (Falconer and Mackay, 1996).

There is a general consensus that inbreeding negatively affects milk production (Hermas et al., 1987; Miglior et al., 1995b; Smith et al., 1998), fertility (Smith et al., 1998; Thompson et al., 2000; Wall et al., 2005), and survival (Smith et al., 1998; Thompson et al., 2000; Sewalem et al., 2006). In Holsteins, effects on milk production generally range from –29.6 to –19.7 kg (Miglior et al., 1995b; Wiggans et al., 1995; Croquet et al., 2006). A 1% increase in inbreeding has also been associated with a lengthening of the calving interval by up to 0.31 d (Fuerst and Sölkner, 1994; Smith et al., 1998).

Nevertheless, the effect of inbreeding on udder health is less conclusive, with some (Miglior et al., 1995a; Biffani et al., 2002; Sørensen et al., 2006) reporting an increase in SCC with inbreeding and others (Smith et al., 1998; Thompson et al., 2000; Gulisija et al., 2007) failing to identify a significant effect of inbreeding on SCC. The effect of inbreeding on cow conformation and calving performance in terms of dystocia, stillbirth, twinning, and sex ratio is less well documented. Adamec et al. (2006) reported increased incidences of dystocia and stillbirth in inbred US Holsteins, whereas others (Smith et al., 1998; Croquet et al., 2006) have documented varying degrees of effects on cow conformation.

Furthermore, few studies have tested whether nonlinear effects of inbreeding on animal performance exist, and these studies have generally been confined to production (Thompson et al., 2000; Croquet et al., 2007; Gulisija et al., 2007), fertility traits (Thompson et al., 2000; Biffani et al., 2002), and udder health traits (Sørensen et al., 2006). In addition, inbreeding depression on economically important traits in dairy cattle

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has never been quantified on a strict seasonally calving grass-based system of milk production, such as exists in Ireland, where fertility plays a greater role in overall herd profitability (Veerkamp et al., 2002). Mc Parland et al. (2007) reported a rate of increase in inbreeding in Irish Holstein-Friesians of 0.10% per year over the past decade, thereby suggesting that inbreeding depression may be evident in Irish dairy herds. The objective of this study was to quantify the effect of inbreeding on a range of performance-related traits in Irish Holstein-Friesian dairy cows.

MATERIALS AND METHODS

Data Edits

Milk production data consisting of 305-d lactation yield records of milk, fat, and protein as well as geometric mean SCC ($n = 876,414$); calving performance data records consisting of incidence of stillbirth, dystocia, twins, and calf sex ($n = 2,821,450$); fertility data records consisting of calving dates and calving interval ($n = 616,653$); and linear type trait data records ($n = 36,210$) were extracted from the Irish Cattle Breeding Federation database for cows calving between 2003 and 2005, inclusive. Records from the years 1990 to 2005, inclusive, were used for the type trait data because of the small size of the data set.

Pedigree information on 2,678,663 Holstein-Friesian animals, including dates of birth, was also extracted from the Irish Cattle Breeding Federation database. Holstein-Friesian animals were defined as all crosses between the Holstein and Friesian breeds, including purebred Holsteins and purebred Friesians (Mc Parland et al., 2007). Inbreeding coefficients (F) were calculated using the Meuwissen and Luo (1992) algorithm with a base year set to 1950. Only performance records for animals with a minimum of 3 complete generations of pedigree information were retained.

Milk Production and SCC. Lactation information from animals of parities 1 to 5 was retained, corresponding to the data used in genetic evaluations in Ireland. Milk, fat, and protein 305-d yields were predicted with standard lactation curve methodology, as outlined by Olori and Galesloot (1999). Age was nested within parity and outlying ages deviating by greater than 24 mo from the median age per parity were removed, as were animals younger than 20 mo at first calving. Contemporary groups of herd-year-season of calving (**HYS**) were created by concatenating herd, year, and month of calving. Where a contemporary group had less than 5 records, adjacent months were merged and HYS was regenerated. Finally, any HYS with less than 3 records was removed.

Lactations shorter than 100 d or longer than 400 d were removed. Outliers for milk production were defined as those greater than 3 standard deviations from the mean and were subsequently removed. The natural logarithm of SCC divided by 1,000 was used to normalize the data; this variable is referred to herein as SCS. The final data set to be used in the analyses contained 138,577 milk lactation records (Table 1), of which 136,950 had SCS information.

Calving Performance. Dystocia is recorded in Ireland on a scale of 1 to 4: 1) unassisted calving, 2) minor assistance, 3) major assistance, and 4) veterinary assistance. For the purpose of this study, dystocia was dichotomized as 0 (no assistance) or 1 (assistance required), where scores of 2, 3, or 4 were classed as "assistance required." Parities greater than 4 were grouped together and parities greater than 10 were removed. Stillbirth was defined as 1 = stillbirth occurred or 0 = no stillbirth occurred. Births coded as abortions were removed, as were any multiple births greater than twins. Contemporary groups of HYS were generated, similar to those described previously for milk production. Two separate data sets were constructed. The first data set was used to quantify the effect of dam inbreeding on calving performance. The second data set was used to investigate the effect of calf inbreeding on calving performance. Twin births were not included when quantifying the effect of inbreeding on calving dystocia, stillbirths, or sex ratio but remained in the data set for determining the effect of inbreeding on twinning rate. Details of the numbers of dam and calf records analyzed are included in Table 1. Fewer calf records than dam records were eligible for analyses because of the mating of Holstein-Friesian dams to predominantly beef sires.

Fertility and Survival. Age at first calving, calving interval from first to second lactation, and survival to second lactation were analyzed. In Ireland, the majority of dairy herds calve cows in the spring, although a small percentage operate a split calving pattern, with a proportion of cows calving in the spring and the remainder calving in the autumn. To avoid potential bias on model solutions because of farmers consciously allowing an extended voluntary waiting period post-calving prior to insemination, only herd-years with at least 80% of animals calving between December and June, inclusive, were retained. Age at first calving was retained where animals calved between 660 and 900 d of age. Only calving intervals to second parity of between 300 and 800 d were retained. Survival to second lactation was treated as a binary variable, where animals who did not survive to second lactation were assumed to be culled (i.e., survival = 0). For the analysis of calving interval and survival, contemporary groups of HYS of calving were generated as described previously,

Table 1. Number of records and mean inbreeding per parity included in the milk production and calving performance analyses

Parity	Milk production		Calving performance			
	Records	Mean F	Dams		Calves	
			Records	Mean F	Records	Mean F
1	47,125	2.76	63,779	2.78	52,761	3.49
2	35,088	2.54	45,312	2.57	42,487	3.13
3	26,071	2.29	33,420	2.34	30,548	2.96
4	18,264	2.04	23,642	2.09	21,385	2.78
5	12,029	1.76	37,682	1.54	32,192	2.36
Total	138,577	2.43	203,835	2.35	179,373	3.03

whereas HYS of birth were generated for the analysis of age at first calving. After all edits, the data set included 30,327 records for age at first calving, 34,614 records for calving interval, and 42,723 records for survival to second lactation.

Conformation and Management Traits. Traits scored included body and rump traits, such as stature, chest width, angularity, body depth, BCS, rump angle, and rump width, as well as udder traits, such as udder depth, udder support, fore udder attachment, rear udder height, rear view teat position, side view teat position, and teat length. Feet and leg traits, such as rear legs set, foot angle, and locomotion, as well as the management traits of temperament and ease of milking were also scored. All traits were scored on a scale of 1 to 9, inclusive, as described by Berry et al. (2004). Data were edited to include only the first record in time on primiparous animals. Contemporary groups of herd-visit (**HV**) were formed by concatenating herd and test-day of visit. Only contemporary groups with at least 5 observations were retained, in accordance with the recommendations proposed by the World Holstein Friesian Federation concerning the international type classification system (WHFF, 2005), leaving 16,090 records eligible for inclusion in the analyses.

Analysis

Preliminary analyses revealed little difference in estimated model solutions with or without accounting for genetic relationships among animals through the numerator relationship matrix. However, all subsequent analyses were undertaken using a sire model with relationships among sires, with the exception of calving performance, where a sire-maternal grandsire model was used. Pedigree files consisted of up to 28,020 non-founder animals.

All analyses were undertaken in ASReml (Gilmour et al., 2004), and statistical significance of all fixed effects, including level of inbreeding, was based on the *F*-test. Inbreeding coefficient was included in the model either

as a continuous variable or as a classification variable: $F = 0$, $0 < F \leq 6.25$, $6.25 < F \leq 12.5$, $12.5 < F \leq 25$, and $F > 25$; $F = 0$ was treated as the reference category. Both linear and quadratic regressions of inbreeding on all traits were tested for significance when inbreeding was treated as a continuous variable. Furthermore, interactions among inbreeding and parity and sex (where applicable) were tested for significance in the model.

The mixed models used were

$$Y1_{ijklmn} = \mu + HYS_i + PAR_j + AGE_k(PAR_j) + DIM_l + F_m + P_m + S_n + e_{ijklmn};$$

$$Y2_{ijkmnop} = \mu + HYS_i + PAR_j + AGE_k(PAR_j) + SEX_o + F_m + P_m + S_n + MGS_p + e_{ijkmnop};$$

$$Y3_{imn} = \mu + HYS_i + F_m + S_n + e_{imn}; \text{ and}$$

$$Y4_{kmmnqr} = \mu + HV_q + AGE_k + STA_{rm} + F_m + S_n + e_{kmmnqr};$$

where $Y1_{ijklmn}$ is lactation milk, fat, and protein yields (kg), fat and protein concentrations, or SCS; $Y2_{ijkmnop}$ is observations of dystocia, stillbirth, sex, and twinning occurrence; $Y3_{imn}$ is days of calving interval or age at first calving and units of survival; $Y4_{kmmnqr}$ is observations for type trait score and milking temperament and speed; μ is the mean of the population; HYS_i is the effect of herd-year-season of calving/birth *i*; PAR_j is the dam parity ($j = 1$ to 5); $AGE_k(PAR_j)$ is the age in months *k*, nested within parity *j*; DIM_l is the DIM ($l = 100$ to 400 d); F_m is the inbreeding coefficient of animal *m*; P_m is the random permanent environmental effect of animal *m*; S_n is the random effect of sire *n*; *e* refers to the random residual effects; SEX_o is the sex of calf ($1 = \text{male}$; $2 = \text{female}$); MGS_p is the random effect of maternal grandsire *p*; HV_q is the effect of herd-visit *q*; and STA_{rm} is the stage of lactation *r* when animal *m* was scored.

Table 2. Percentage of animals in each inbreeding class across the different analyses

Inbreeding class	Milk production	Calving performance		Fertility + survival	Type traits
		Dams	Calves		
Average F	2.43	2.35	3.03	2.74	3.05
F = 0	3.97	5.31	2.49	2.66	1.42
0 < F ≤ 6.25	91.26	89.96	91.27	91.65	91.37
6.25 < F ≤ 12.5	4.08	4.03	5.16	4.82	6.56
12.5 < F ≤ 25	0.50	0.52	0.76	0.61	0.58
F > 25	0.19	0.18	0.32	0.26	0.07

RESULTS AND DISCUSSION

The mean levels of inbreeding across the data sets varied from 2.35 to 3.05% (Table 2), which are greater than the population average of 1.48% for Holstein-Friesians born in 2004 (Mc Parland et al., 2007). This is due to the greater level of pedigree completeness required for animals to be included in the current analyses. Despite more than 94% of all animals being inbred, only a small proportion of animals had inbreeding coefficients greater than 6.25% (Table 2), with a maximum inbreeding coefficient in any data set of 33.13%.

Milk Production and SCS

Mean (standard deviation) milk, fat, and protein yields and SCS across the entire data set were 7,099 (1,480), 265 (57), and 236 (47) kg, and 4.71 (0.85) SCS units, respectively. Tables 3 and 4 summarize the effect of inbreeding on milk production and SCS. All yield traits decreased ($P < 0.01$) with inbreeding. When inbreeding was treated as a continuous variable, its effect on milk yield was nonlinear, with a greater negative impact at higher inbreeding levels. Inbreeding also had a nonlinear effect on milk protein concentration: low levels of inbreeding resulted in a decrease in protein concentration, whereas higher levels of inbreeding

(>18%) resulted in a rise in protein concentration. Although the nonlinear results reported in this study are statistically significant, all nonlinear results in any dairy cattle population should be interpreted with slight caution because of the paucity of animals with very high inbreeding coefficients (Table 2). However, the effect of inbreeding on milk production when treated as a class variable generally supported the results from the quadratic model. When inbreeding was treated as a class variable, animals with low inbreeding coefficients of between 0 and 6.25% were not significantly affected compared with noninbred animals ($F = 0$). However, as inbreeding increased from 6.25 to 12.5%, a considerable decline in milk yield (47 kg) was observed, whereas milk yield was reduced by 161 kg in animals with inbreeding coefficients of between 12.5 and 25%. In the present study, inbreeding depression associated with an animal 12.5% inbred (i.e., progeny following the mating between noninbred half-sibs) was ≤2% of the mean across the production traits.

The effect of inbreeding on protein yield and milk fat concentration differed ($P < 0.05$) across parities (Table 4). The negative impact of inbreeding on protein yield was greater in multiparous animals. However, a reverse trend was observed with milk fat concentration in that the negative impact was greater in younger

Table 3. Model solutions (SE in parentheses) for the effect of inbreeding on milk, fat, and protein yields (kg), milk fat and protein concentrations ($\% \times 10^3$), and SCS (SCS units $\times 10^2$)

Item	Milk yield	Fat yield ¹	Fat concentration ²	Protein yield ²	Protein concentration	SCS ²
Inbreeding as a continuous variable						
Linear	0.03 (2.56)	-0.4 (0.06)	—	—	-1.6 (0.52)	—
Quadratic	-0.4 (0.15)	—	—	—	0.1 (0.03)	—
Inbreeding as a class variable						
0 < F ≤ 6.25	6.8 (16.74)	1.9 (0.67)	24.3 (7.39)	0.2 (0.51)	2.0 (3.44)	7.6 (1.41)
6.25 < F ≤ 12.5	-47.5 (21.98)	-0.9 (0.88)	15.3 (9.66)	-1.9 (0.68)	-0.1 (4.50)	10.8 (1.85)
12.5 < F ≤ 25	-160.9 (43.12)	-6.0 (1.72)	5.9 (18.89)	-4.8 (1.32)	15.1 (8.80)	2.4 (3.65)
F > 25	-172.5 (67.70)	-4.8 (2.70)	50.6 (29.51)	-5.9 (2.08)	7.9 (13.75)	14.6 (5.74)

¹No significant quadratic effect of inbreeding on fat yield was observed when inbreeding was treated as a continuous variable; thus, only the linear solution is provided.

²When treated as a continuous variable, the effect of inbreeding on fat concentration, protein yield, and SCS differed significantly across parities; therefore, effects are included in Table 4.

Table 4. Model solutions (SE in parentheses) for the effect of inbreeding when interacting with parity on protein yield (kg), fat concentration ($\% \times 10^3$), and SCS (SCS units $\times 10^2$), and the statistical significance of the interactions

Item	Protein yield	Fat concentration	SCS
<i>P</i> -value	0.005	0.039	<0.001
Parity 1	-0.1 (0.06)	-3.8 (0.76)	0.2 (0.16)
Parity 2	-0.3 (0.06)	-2.0 (0.83)	0.9 (0.19)
Parity 3	-0.4 (0.08)	-1.8 (0.96)	1.0 (0.22)
Parity 4	-0.4 (0.09)	-0.2 (1.17)	1.2 (0.27)
Parity 5	-0.4 (0.12)	0.2 (1.51)	1.5 (0.35)

animals, although mean fat concentration was also greatest in first-parity animals.

In agreement with the present study, a similar curvilinear effect of inbreeding on milk production was reported in US Holsteins (Thompson et al., 2000), US Ayrshires (Hudson and Van Vleck, 1984), and US Jerseys (Miglior et al., 1992). In direct contrast, however, the quadratic effect of inbreeding on milk production also observed by Croquet et al. (2007) in Walloon Holsteins was manifested as less deleterious effects at higher levels of inbreeding. Little information is available regarding the effects of inbreeding on milk fat and protein concentrations in Holsteins (Miglior et al., 1995b); however, studies in pluriparous cows of alternative breeds excluding Holsteins (Casanova et al., 1992; Fuerst and Sölkner, 1994) have reported mixed effects of inbreeding on milk fat and protein concentrations.

The deleterious effect of inbreeding on milk production, although in agreement with previous literature, was generally less than most previously reported estimates (Wiggans et al., 1995; Smith et al., 1998; Croquet et al., 2006), although low estimates of inbreeding depression on 305-d milk yield (-9.8 kg) have also been reported in Jersey cattle (Miglior et al., 1992). Inbreeding may, however, be considered relative to production (Fuerst and Sölkner, 1994); average 305-d yield for animals in the present study was 7,099 kg compared with the 8,794 kg mature equivalent for US Holsteins reported by Smith et al. (1998). Furthermore, rates of accumulation of inbreeding are likely to affect inbreeding depression. Falconer and Mackay (1996) stated that a rapid rise in inbreeding will result in greater inbreeding depression. The rate of increase in inbreeding in Irish Holsteins is 0.10% per annum (Mc Parland et al., 2007), which is slower than the increase of 0.15% per annum estimated from fitting a linear regression to annual inbreeding levels in the United States across the same time period (Animal Improvement Programs Laboratory, 2007). Additionally, the nonlinear effect of inbreeding on milk production in the present study indicates that the effect of inbreeding is dependent on

the levels compared. For example, the marginal decrease in 305-d milk yield by increasing inbreeding from 25 to 26% was 20 kg, which is more consistent with previous estimates (Casanova et al., 1992; Croquet et al., 2006).

Inbreeding increased SCS in the present study, with the effect being greater in older animals (Table 4). Inbreeding depression for SCS equated to an increase in SCC of 23,000 cells/mL above the mean for a fifth-lactation animal 12.5% inbred. The inbreeding depression associated with a 12.5% inbred animal represented 2.6% of the mean and 2.5% of the additive genetic standard deviation. Several studies have attempted to quantify the effect of inbreeding on SCS and have either found no significant effect (Smith et al., 1998; Thompson et al., 2000; Gulisija et al., 2007) or reported low levels of inbreeding depression for SCS (Miglior et al., 1995a; Biffani et al., 2002; Mrode et al., 2004). Miglior et al. (1995a) reported a linear increase of 0.012 SCS units in lactation average SCS per 1% inbreeding in primiparous Canadian Holsteins; however, the SCS reported by Miglior et al. (1995a) were transformed by using the logarithm to the base 2. The effect of inbreeding on SCS in the present study was linear, which is at odds with the significant nonlinear effect of inbreeding on SCS in primiparous Danish Holsteins (Sørensen et al., 2006). Because SCS is an indicator of mastitis (Mrode and Swanson, 1996), results from the current study suggest that inbreeding may also increase the incidence of mastitis. No information on clinical mastitis was available in the current study; however, Sørensen et al. (2006), using data on clinical mastitis, did report a higher incidence of clinical mastitis in inbred animals.

Calving Performance

The effect of dam inbreeding and calf inbreeding were studied separately because both maternal and fetal effects may influence calving performance (Adamec et al., 2006). However, the authors are unaware of any study that has attempted to quantify the effect of fetal inbreeding on calving dystocia and stillbirth incidence. Incidences of dystocia and stillbirths in both data sets were 32 to 33% and 4 to 5%, respectively. Incidence of twins in both data sets was 2.5%, but neither calf nor dam inbreeding significantly affected the twinning rate.

The effect of dam inbreeding on dystocia in the present study did not differ by parity or sex of calf. Dystocia increased with the level of dam inbreeding up to 25%, at which point it reversed ($P < 0.001$; Figure 1), possibly because of inbred dams producing smaller calves. Another reason may have been that fetuses from highly inbred dams, where calving difficulty may have been

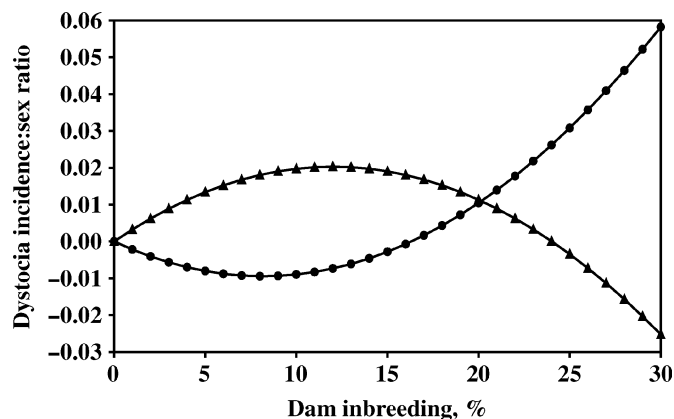


Figure 1. Effect of dam inbreeding on dystocia incidence ($P < 0.001$; \blacktriangle) and sex ratio ($P < 0.05$; \bullet). Sex ratio < 0 = increased numbers of male births; sex ratio > 0 = increased numbers of female births.

expected, could have died in utero or been aborted prior to full term and therefore did not receive a score for dystocia. Pulkkinen et al. (1998) reported an apparent effect of dam inbreeding on increased fetal mortality in early gestation. Nonetheless, the increased risk of dystocia in moderately inbred animals observed in the present study may be due to smaller dam size at calving; Young et al. (1969) reported lower live weights at 2 yr of age in inbred animals. Similar to when inbreeding was treated as a continuous variable, dams with inbreeding coefficients of between 0 and 12.5% had a 1% greater incidence of dystocia when estimated by treating inbreeding as a class variable, whereas dams with inbreeding coefficients of between 12.5 and 25% had a 3% greater incidence of dystocia over noninbred dams. Adamec et al. (2006) also reported small effects of inbreeding on calving difficulty, justifying the slight effect of inbreeding depression on potentially undersized calves being born from inbred dams; however, Adamec et al. (2006) defined calving dystocia as calvings with more than a “slight problem.”

Calf inbreeding did not affect ($P > 0.05$) dystocia in the present study, although the trend was toward a reduction in dystocia with increased calf inbreeding, which may also have been due to inbred calves being potentially smaller in size. Young et al. (1969) reported lower calf birth weights of 0.11 kg per unit increase in inbreeding.

Dam inbreeding resulted in a greater incidence of stillbirths, of 0.06% (SE = 0.02%) per 1% increase in inbreeding, which is within the range of inbreeding depression reported by Adamec et al. (2006) in US Holsteins; the effect did not differ significantly across dam parity or calf sex in the present study. However, the effect of calf inbreeding on stillbirth incidence in the

present study was parity dependent ($P < 0.01$) but was consistent across both sexes. Stillbirth incidence increased with calf inbreeding in primiparous animals at a rate of 0.2% (SE = 0.04%) per 1% increase in inbreeding, whereas the effect of inbreeding on multiparous animals was lower and not significantly different from zero. The greater effect of calf inbreeding on stillbirths in primiparous animals is somewhat in agreement with the report by Adamec et al. (2006) of a greater effect of dam inbreeding on stillbirths in primiparous animals.

The inclusion of dystocia as a fixed effect in the model had a negligible effect on the regression coefficients when investigating the effect of inbreeding on stillbirth incidence, but was excluded from the final model used for the analyses because it may have accounted for some of the true effect of inbreeding on stillbirths, given the significant effect of inbreeding on dystocia reported in the present study. Overall, in agreement with Adamec et al. (2006), inbreeding did not appear to be a major contributor to dystocia and stillbirth in Holstein dairy cows. Nevertheless, such effects may result in an underestimation of inbreeding depression in other performance traits, because the inbred animals that die at birth (or prior to first calving) may also be predisposed to poorer performance but do not have the opportunity to express these traits.

Figure 1 illustrates the nonlinear effect of dam inbreeding on sex ratio. Dams of moderate inbreeding levels (5 to 10%) had, on average, 1% more males than noninbred dams. In contrast, dam inbreeding levels of $> 16\%$ altered the sex ratio in favor of female births ($P < 0.05$); dams with inbreeding levels of 25% are expected, on average, to give birth to 3% more females than are noninbred dams. This phenomenon may be associated with the hypothesis of Trivers and Willard (1973) that as maternal condition declines (i.e., greater inbreeding), the secondary sex ratio shifts in favor of female births. Several studies have been conducted illustrating the effect of dam stress on the secondary sex ratio (Trivers and Willard, 1973; Roche et al., 2006). Nonetheless, the authors are unaware of any study that has related inbreeding to sex ratio in dairy cattle. Nor are the authors aware of any study that has shown the effect of stress on the neonate through all stages of development (even prior to the sex-determination stages) on sex ratio, as may be the case for an inbred calf. Increases in calf inbreeding in this study were linearly ($P < 0.05$) associated with an increase in the proportion of male births; the incidence of male calves was 0.1% greater per percentage unit increase in calf inbreeding. Thus, when 2 closely related animals (whether inbred or not) are mated, there is a greater probability that the resulting offspring will be male. This may be a result of the secondary sex ratio of inbred

Table 5. Model solutions (SE in parentheses) for the effect of inbreeding, when fitted as a continuous variable in a linear or quadratic model, on fertility (d), survival (%), and cow conformation (units $\times 10^3$; scale 1–9)

Item	Linear	Quadratic	<i>P</i> -value ¹
Fertility and survival			
Calving interval	0.7 (0.21)	—	0.001
Age at first calving	0.2 (0.08)	—	0.005
Survival	-0.3 (0.10)	—	0.006
Conformation			
Udder			
Udder depth	31.9 (8.41)	-1.4 (0.58)	<0.001
Rear udder height	36.3 (9.41)	-1.7 (0.65)	<0.001
Udder support	28.7 (9.41)	-1.4 (0.65)	0.006
Fore udder attachment	33.3 (9.84)	-1.6(0.68)	0.002
Teat length	13.9 (4.65)	—	0.003
Teat position, rear view	7.3 (5.15)	—	0.157
Teat position, side view	-5.3 (4.20)	—	0.207
Frame and capacity			
Angularity	58.1 (8.11)	-2.6 (0.56)	<0.001
Chest width	-61.3 (10.38)	2.6 (0.71)	<0.001
BCS	-66.6 (11.17)	3.2 (0.77)	<0.001
Rump width	-16.2 (4.78)	—	0.001
Stature	25.2 (7.72)	-1.5 (0.53)	0.005
Rump angle	5.2 (4.37)	—	0.238
Body depth	1.2 (4.19)	—	0.777
Feet and legs			
Rear legs set	7.3 (4.08)	—	0.074
Foot angle	-3.6 (4.82)	—	0.458
Locomotion	-1.4 (4.48)	—	0.764
Management			
Ease of milking	-7.1 (4.31)	—	0.098
Temperament	-2.9 (3.82)	—	0.454

¹Where quadratic solutions are significant, *P*-values represent the cumulative significance of linear and quadratic solutions; otherwise *P*-values represent the significance of the linear solution.

animals being altered at fertilization (the sex-determination stage) or of preferential embryo or fetal mortality in utero.

Fertility and Survival

Optimal fertility is paramount for maximizing profitability in seasonally calving herds, as are predominantly operated in Ireland. Farmers require compact calving; therefore, animals with delayed first calving or a longer calving interval have a greater risk of involuntary culling. Nonetheless, this is the first study to investigate the effect of inbreeding on fertility and survival in seasonally calving grass-based systems of milk production. In this study, only calving interval and survival to second lactation were analyzed to avoid any potential bias of inbreeding on reappearance in second lactation, as well as to ensure that animals included in the analyses had the opportunity to express each trait. Mean age at first calving, calving interval, and survival to second lactation were 763 d, 404 d, and 0.74, respectively.

Inbreeding had an unfavorable linear effect ($P < 0.01$) on all 3 traits analyzed (Table 5). From these results,

it may be determined that a cow 12.5% inbred (born following the mating of noninbred half-siblings) is expected to have, on average, a longer calving interval of 8.8 d, be 2.5 d older at first calving, and have a 4% lower survival to second lactation.

Furthermore, the deleterious effects of longer calving intervals accumulate over parities in seasonally calving herds, thereby leading to a shift in the overall herd calving pattern to less profitable months of the year. The effect is further exacerbated by replacement heifers being born later, and thus either calving at younger ages or calving later in the year. Veerkamp et al. (2002) used transition matrices to model the impact of a 1-d longer calving interval on herd calving pattern when equilibrium was reached.

The inbreeding depression experienced by a cow with inbreeding of 12.5% (following the mating of noninbred half-sibs) was 0.36, 2.09, and 4.35% of the mean for age at first calving, calving interval, and survival, respectively. When expressed as a proportion of the additive genetic standard deviation of the respective traits, inbreeding depression equated to 1.2 to 1.6% for these traits; the corresponding values for milk, fat, and protein yields were 3.6 to 8.1% of the additive genetic standard deviation and for milk concentration were 15.6 to 21.9% of the additive genetic standard deviation. Therefore, this suggests that the level of inbreeding depression is greater in the milk production traits, which is at odds with the expectation that inbreeding depression would be greater in traits associated with fitness and survival (Falconer and Mackay, 1996). Nevertheless, milk production may be considered a “fitness” trait because it is the primary energy source for the growth of a calf.

Smith et al. (1998), corroborating results from the present study, reported reduced days of productive life (-5.96 d/percent inbreeding) and greater calving interval (0.31 d/percent inbreeding) and age at first calving (0.55 d/percent inbreeding) in inbred animals. Furthermore, Biffani et al. (2002) and Wall et al. (2005) in Italian and UK Holsteins, respectively, also reported lower unfavorable effects of inbreeding on calving interval than reported in this study, whereas Hoeschele (1991) and Biffani et al. (2002) reported an increase in days open (a trait strongly correlated to calving interval) of 0.13 and 0.31 d/percent inbreeding, respectively. In further agreement with the present study, Sewalem et al. (2006) reported an increased risk of being culled as the level of inbreeding increased. The lack of any significant nonlinear effects in the present study disagrees with the results of Thompson et al. (2000) and Biffani et al. (2002), both of whom reported a nonlinear effect of inbreeding on age at first calving, with only

inbreeding levels greater than 10 and 16%, respectively, having an unfavorable effect on age at first calving.

Cow Conformation and Management Traits

Inbreeding did not have a significant effect on ease of milking or temperament, nor did it affect body depth, rump angle, locomotion, rear leg, foot angle, or teat position (Table 5). Nevertheless, inbreeding did have a significant effect on some body- and udder-related traits. As inbreeding increased, all udder traits, with the exception of side and rear view teat positions (for which inbreeding showed no significant effect), displayed an increase in score. However, effects were mostly nonlinear, ranging from an increase in score of 0.15 to 0.19 for animals with 12.5% inbreeding (Table 5). Teat length was the only udder-related trait that was linearly affected by inbreeding, with teats expected to lengthen by 0.01 units per 1% increase in inbreeding. Smith et al. (1998) and Biffani et al. (2002) also reported positive regressions of score on inbreeding for most udder traits, although differences in the traits analyzed existed across studies.

The effect of inbreeding on most body traits was also nonlinear (Table 5). Moderately inbred animals (i.e., 0 to 17% inbred) were taller and more angular with narrower chests, although the reverse was true in highly inbred animals; the standard errors of the higher estimates were expected to be large, given the paucity of extremely inbred animals. One factor contributing to the effect of inbreeding depression on type traits observed in the present study may be linebreeding, where voluntary inbreeding may be practiced to achieve desirable cow conformation, such as tall and angular animals with good udder support and attachment. In contrast to the results from the present study, Smith et al. (1998), using mixed linear models, documented that inbred animals were characterized as being smaller and shallower. Croquet et al. (2006) also documented that inbred Holsteins tended to be smaller, narrower, and shallow bodied.

CONCLUSIONS

Inbreeding had a deleterious effect on milk production, udder health, calving performance, fertility, and survival. Although the effects of inbreeding reported in this study were small, and are unlikely to cause great financial loss on Irish dairy farms for most traits, the impact on fertility and survival was relatively large, given the cumulative effect that age at first calving and calving interval has on herd calving patterns in seasonally based calving herds. Furthermore, the rise in inbreeding in the population suggests that selection

of young test sires will have to take into account co-ancestry with the current population. The nonlinear effect of inbreeding on most milk production, calving performance, and type traits suggests that epistatic effects might also play a role in inbreeding depression (Falconer and Mackay, 1996), although the effect of inbreeding on fertility and survival were all linear, suggesting that partial dominance or overdominance are the main genetic mechanisms through which inbreeding affects these traits (Falconer and Mackay, 1996).

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