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Genetics of reproductive performance in seasonal calving dairy cattle production systems

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Profitable seasonal calving dairy production systems require a cow that will establish pregnancy early in the breeding season implying a quick return to service post-calving and good pregnancy rates. Genetic selection provides an opportunity to achieve this goal so therefore the objective of this study was to estimate the necessary genetic parameters for fertility traits, pertinent to seasonal calving herds, in order to facilitate genetic selection for fertility. The data, following editing, consisted of parity 1 to 3 records on up to 397,373 Holstein-Friesian dairy cows in Ireland. Variance components for the defined interval fertility traits (age at first calving, calving to first service interval, calving interval), binary fertility traits (submission rate in the first 21 days of the breeding season, pregnant to first service, pregnant in the first 42 days of the breeding season, calved in the first 42 days of the calving season) and the count fertility trait (number of services) were estimated using univariate animal models and covariances among traits were estimated using bivariate sire models. Heritability estimates of the nine fertility traits (including age at first calving and survival) varied from 0.01 to 0.07 within parity one to three. The coefficient of genetic variation for the fertility traits varied from 3.3% to 15.3%. Calving to first service interval, within parity, was moderately positively genetically correlated (0.54 to 0.75) with calving interval and was, in general, moderately negatively correlated with both submission rate (-0.68 to -0.29) and pregnant in the first 42 days of the breeding season (-0.36 to -0.14). Calving interval was moderately positively correlated (0.24 to 0.68) with number of services. Irrespective

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of parity, the genetic correlations between calving interval with calving in the first 42 days of the calving season, and submission rate with pregnant in the first 42 days of the breeding season were all negative. The genetic correlations among calving in the first 42 days of the calving season, submission rate and pregnant in the first 42 days of the breeding season were all positive. All fertility traits were generally antagonistically genetically correlated with lactation milk yield, but most were moderate to strongly favourably correlated with survival to the next lactation. This study provides the necessary genetic parameters to undertake national genetic evaluations for fertility to help achieve the fertility targets in seasonal calving herds.

Keywords: dairy; fertility; heritability; Holstein-Friesian

Introduction

There is a general consensus that the heritability for fertility traits is low, with most heritability estimates of traditional measures of fertility being <5% (Pryce and Veerkamp 2001; Wall *et al*. 2003; Jamrozik *et al*. 2005); heritability estimates for fertility traits derived using hormonal assays tend to be greater (Royal *et al*. 2002; Veerkamp, Koenen and de Jong 2001; Berry *et al*. 2012). To-date however, with the exception of a few studies (Grosshans *et al*. 1997; Pryce and Harris 2006; Olori, Meuwissen and Veerkamp 2002; Haile-Mariam, Morton and Goddard 2003), most of the reported genetic parameters for fertility traits have been estimated from animals in year-round calving milk production systems. Firstly, traits different to those previously evaluated in year-round calving systems may be more pertinent to seasonal calving production systems such as the ability to calve early in the calving season. Secondly, the phenotypic and genetic variation (and potentially their ratio) in some traits may differ with production system; for example in a seasonal calving herd strong emphasis is placed on the ability of the cow to return to service early post-calving while extended voluntary waiting periods may be tolerated in non-seasonal herds. Finally, covariances among fertility traits and between fertility traits and milk production may differ depending on the milk production system. The latter has particular implications with the exploitation of genomic selection (Meuwissen, Hayes and Goddard 2001) which is expected to increase the rate of genetic gain considerably (Pryce *et al*. 2010).

Seasonal calving systems are characterised by cows calving over a relatively short period of time; in Ireland some seasonal calving herds include herds that calve a portion of the herd in spring and the remainder in autumn. The rationale for seasonal calving in spring is to synchronise the start of lactation with the initiation of grass growth thereby maximising the utilisation of grazed grass in the diet (Dillon *et al*. 1995). In 2007, 80% of calves born in Ireland to a dairy sire were born in the months of January to April, inclusive (Department of Agriculture, Fisheries and Food 2008). By definition, seasonal calving also implies seasonal breeding. Therefore, traits evaluated for use in a seasonal calving production system must take cognisance of the importance of submission for service early in the breeding season (irrespective of when the cow calves) as well as the ability to conceive and maintain a pregnancy.

The objective of the present study was to document average phenotypic performance as well as estimate genetic parameters for a range of fertility traits pertinent to a seasonal calving dairy herd. Results from this study will be useful in benchmarking mean phenotypic fertility performance in Ireland against targets as well as international seasonal calving systems of production. Estimates of genetic parameters will be useful to determine the feasibility of genetically improving the various traits as well as facilitating a greater understanding of the genetic associations between the different measures of fertility.

Materials and Methods

Data on artificial (n=2,938,382) and natural mating (n=277,568) service records as well as pregnancy diagnoses information (n=494,955) from 2,060,784 lactations on 1,022,329 Holstein-Friesian cows in 16,904 dairy herds across the years 2002 to 2010, inclusive were extracted from the Irish Cattle Breeding Federation database. Obvious data errors (e.g., service date earlier than date of birth) were removed. The distribution of these data throughout the year is illustrated in Figure 1. Where two service records for the same cow were within 5 days of each other, only the last record in time was retained. However, the occurrence of these multiple inseminations was recorded for use in the final analysis; 72,327 service records were discarded. Data from parities greater than 3 were discarded. Additionally, only data prior to one calendar year before a cow was used in an embryo transfer programme were retained.

A range of fertility variables were derived which may broadly be classified into 1) interval traits, 2) binary traits, and 3) count traits.

Interval fertility traits

Calving to first service interval (CFS) was defined for all cows as the number of days from calving to first service and only CFS records between 10 and 250 days were retained. Calving interval (CIV) was defined as the number of days between consecutive calvings. Where no service data were available, only CIV records between 300 and 600 days were retained; if CFS was <150 days then CIV between 300 and 800 days were retained. Calving to conception interval was not included in the present study since it is strongly correlated with CIV and date of conception was not available for most cows since, in Ireland, natural mating tends to be used after the artificial insemination (AI) breeding season; natural mating events are generally not reliably recorded. For the same reason the interval from first service to last insemination or conception was also not considered in the present study. Most of the variation in these traits is expected to be captured by number of services (discussed later); however, unlike the aforementioned traits, observations for number of services exist even for cows that did not conceive.

Age at first calving (AFC) was also defined although it could be argued that this trait may be more a reflection of growth and maturity rather than fertility *per se*. Only records for AFC of between 660 and 1,240 days were retained.

Binary fertility traits

Binary traits relating to submission rate (SR), pregnancy rate, and calving rate were defined. Seasonal calving production systems are characterised by, as well as cows calving within a period of the calendar year, cows being served within a period of the calendar year. Because of the decline in fertility in Irish dairy herds (Evans *et al.* 2006) and the cost of replacements, not all cows in Irish herds calve, or are bred, within a strict time period. Therefore in the present study the start of the breeding season was defined as the date when five pluriparous animals were served within the

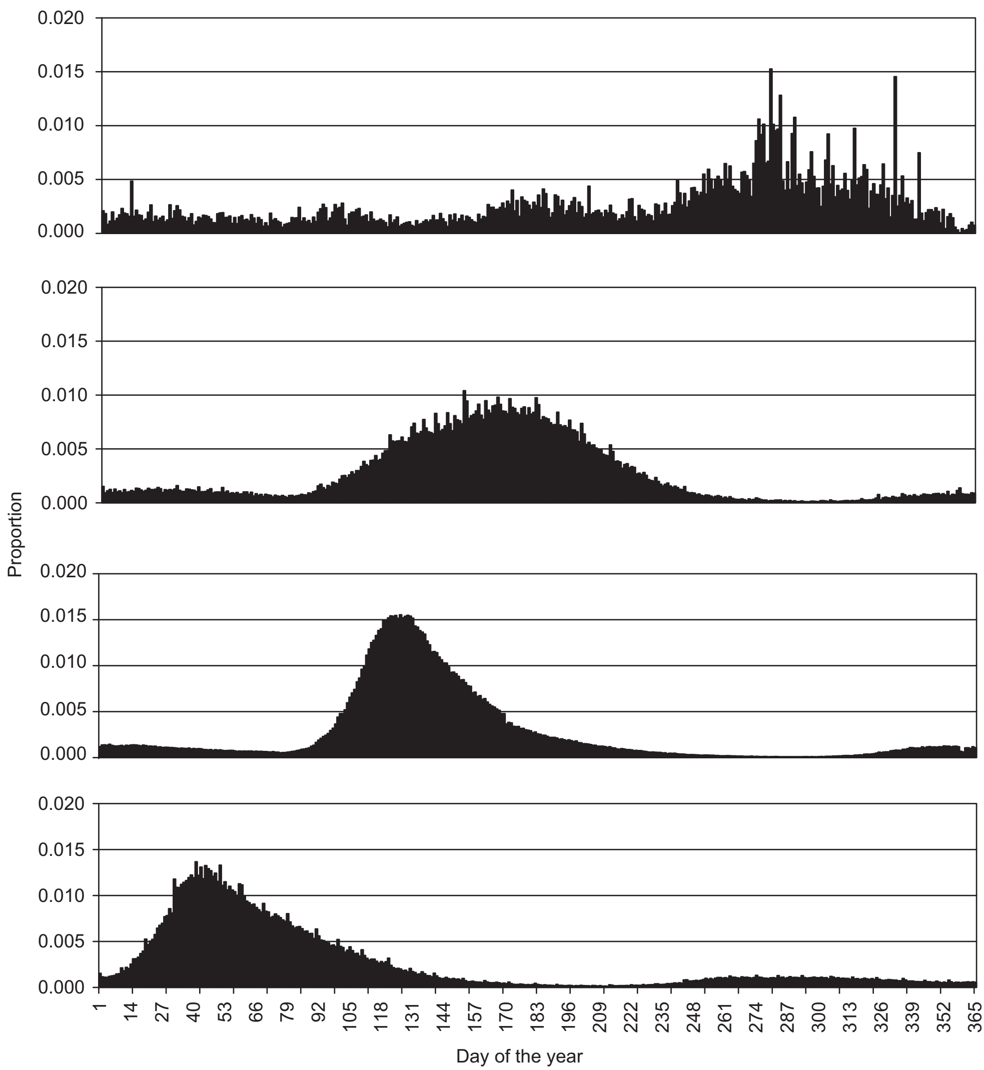

Figure 1. Frequency distribution across days of the year from bottom to top are: calving events, AI services, natural services and pregnancy diagnosis events.

subsequent 14 days. Data on nulliparous animals were not included when defining the start of the breeding season as in Ireland, nulliparous heifers are generally mated earlier than cows. The end of the breeding season was defined as the last service within a herd which was not followed by a subsequent service within 21 days. Only breeding seasons spanning between 35 and 140 days with at least 20 pluriparous cows were retained. The start of the calving season was defined using similar methodology, in that the calving season was deemed to have commenced when five consecutive calving events were within 14 days of each other. Calving seasons were defined separately for primiparae and pluriparae. Only calving seasons between 35 and 200 days in length were retained. When defined for primiparous cows, only calving seasons with at least 6 calving events were retained; when defined for pluriparous cows only calving seasons with at least 20 calving events were retained.

Submission rate in the present study was defined as whether or not a cow, irrespective of her calving date, was served for the first time in the first 21 days of the breeding season; SR for cows not served for the first time during a predefined breeding season were set to missing.

Calving rate in the first 42 days of the calving season (CALV42) was defined as whether or not a cow calved in the first 42 days of the calving season where the start of the calving season was as previously described. As previously mentioned, a separate calving season was defined for primiparae and pluriparae. Records for CALV42 cows not calving during a calving season were set to missing with the exception of cows that calved within 14 days prior to the start of the calving season; these cows were deemed to have calved in the first 42 days and this edit was included to account for premature births or short gestations.

Pregnant in the first 42 days of the breeding season (PR42) was defined as whether or not a cow became pregnant in the first 42 days of the breeding season; this trait was not defined in heifers. Only data from breeding seasons where AI was used and the length of the AI breeding season was at least 42 days were retained. Cows that had a recorded service date (either artificial or natural) after day 42 of the breeding season were coded as not PR42. Cows served within 30 days of the end of the AI season or within 30 days of being sold were coded as missing unless they had a recorded service after day 42 of the breeding season where they were coded as not pregnant, or where they had a subsequent calving date confirming, based on the calculated gestation length, that they were pregnant in the first 42 days of the breeding season. Norman *et al*. (2009) reported a mean gestation length of 278 to 279 days in Holstein heifers and cows, respectively, with a standard deviation of 5.5 to 5.7 days. Therefore acceptable gestation lengths used in the present study were between 265 and 295 days when the mated sire was Holstein-Friesian and between 265 and 300 days when the mated sire was not Holstein-Friesian since gestation length tends to be longer in some beef breeds (Mujibi and Crews 2009). Cows calving more than 248 days from the start of the previous breeding season were coded as not PR42. Pregnancy diagnosis data were also used, where subsequent calving dates were not available, to further attempt to determine if the cow was pregnant in the first 42 days of the breeding season. Where no subsequent calving date was available, and the cow had no recorded service after 42 days of the breeding season but was diagnosed as being pregnant, then the cow was deemed to have become pregnant in the first 42 days.

Pregnancy rate to first service (PRFS) was defined to represent a conception trait. Because some natural services are inadvertently not recorded, PRFS was only defined within herds that used some AI and only first service records during the breeding season were used. If the cow had a recorded service within 30 days of the end of the AI breeding period or her date of culling, then she was coded as missing for PRFS. However, where a second service was recorded then the cow was assumed not to have conceived to first service (i.e., PRFS=0). Cows pregnancy diagnosed as not pregnant were coded as not PRFS. Subsequent calving dates, if available, were also used when defining PRFS, as outlined in the definition of PR42.

Count fertility traits

Number of services (NS) was the only count trait defined and was defined as the number of services a cow received within each lactation; cows that received more than ten services in a lactation were given a value of ten. To remove herds that only record the last insemination, herd-years where >80% of cows were recorded as having received only one service were discarded for all fertility traits.

Survival and milk production traits

Phenotypes for milk production and survival were as currently defined in the Irish national genetic evaluation. Lactation (i.e., 305-day) milk, fat and protein yield are estimated for each parity by a method of interpolation using previously derived lactation curves for Irish Holstein cows (Olori and Galesloot 1999). This method computes 305-day yield separately for milk, fat and protein yield in each parity based on test-day yields and also utilises information from the previous lactation when present. If a cow had a recorded calving date for lactation i, then it was assumed to have survived lactation i-1. A cow was assumed not to have survived lactation i if she did not have a calving record for lactation $i+1$ and the difference between her last recorded milk test-day was >140 days from the last recorded milk test-day for that herd.

Fixed effects

Prior to the generation of contemporary groups, only cows born within 8 years of the birth of their sire were retained. Furthermore, only cows with four additional paternal-half sibs were retained. An algorithm was invoked to generate contemporary groups pertinent to each of the traits based on the procedures similar to those described by Schmitz, Everett and Quaas (1991) and Crump *et al*. (1997). The algorithm is based on grouping animals together, within herd, that have dates in close proximity; for heifer traits (i.e., AFC and CALV42) date of birth was used as the date variable, while calving date was used for the fertility and production traits in pluriparae. Initially dates differing by a pre-defined number of days (in this study 10 days was chosen) were placed in separate contemporary groups. Subsequently, if the number of records within any contemporary group was less than a predefined number (6 was chosen in the present study) they were merged with a contemporary group adjacent in time if the start date and end date of the adjacent contemporary groups was less than a specified number (in this study 152 days was used as the threshold). Subsequently only contemporary groups with at least 5 animals were retained. Because of differences in the data available for each animal, contemporary groups for animals, within parity, were defined for AFC and CALV42 together in heifers, for CFS, CALV42, and NS together, and then separately for PRFS, PR42, CIV, and survival.

Age at calving was calculated for each calving and was expressed relative to the median within parity. Records where cows calved greater than 2 years from the parity median were discarded. Heterosis and recombination loss coefficients were calculated for each animal as described by Akbas, Brotherstone and Hill (1993)

$$\text{heterosis} = P_S(1\text{-}P_D) + P_D(1\text{-}P_S)$$
$$\text{recombination loss} = P_D(1\text{-}P_D) + P_S(1\text{-}P_S)$$

where P_S and P_D are the proportion Holstein in the sire and dam, respectively.

Analysis

Prior to the estimation of variance components a random sample of contemporary groups was chosen, within trait and parity, to result in a dataset with, where possible, approximately 100,000 records per trait. Many traits had less than 100,000 records and therefore a random sample was not taken. Numbers of records per trait are summarised in Table 1.

Variance components for the fertility traits were estimated, within each parity separately, using an animal mixed model in ASREML (Gilmour *et al*. 2009) with the relationships among all animals included via the relationship matrix. All animals were traced back at least four generations where available. Covariances among traits were estimated using a series of bivariate sire models including relationships among sires. Fixed effects considered for inclusion in all models were contemporary group, Holstein proportion of the cow, age relative to the parity

Table 1. Number of records, mean, genetic standard deviation (S_g) and heritability (h^2; standard errors in parentheses) for the different fertility traits evaluated in parity one to three cows

Trait	Parity	No	Mean	S_g	h^2
Age at first calving		60330	797	36.1	0.07 (0.011)
Calving to first service interval	1	73695	82	6.8	0.07 (0.009)
	2	58577	78	5.3	0.04 (0.008)
	3	43548	75	4.7	0.03 (0.008)
Calving interval	1	112289	402	13.7	0.03 (0.005)
	2	82909	398	15.3	0.04 (0.006)
	3	100700	393	12.9	0.03 (0.006)
Number of services	1	73695	1.68	0.46	0.03 (0.007)
	2	58577	1.70	0.46	0.04 (0.008)
	3	43548	1.70	0.46	0.04 (0.009)
Pregnant to first service	1	48279	0.47	0.46	0.01 (0.005)
	2	38792	0.44	0.45	0.01 (0.006)
	3	29081	0.43	0.46	0.02 (0.008)
Submission in the first 21 days of the breeding season	1	55418	0.64	0.42	0.02 (0.006)
	2	45161	0.62	0.43	0.04 (0.008)
	3	33932	0.62	0.44	0.03 (0.009)
Calving in the first 42 days of the calving season	1	76419	0.76	0.37	0.01 (0.005)
	2	53995	0.66	0.39	0.01 (0.004)
	3	40984	0.62	0.42	0.02 (0.007)
Pregnant in the first 42 days of breeding seasons	1	48228	0.61	0.08	0.03 (0.007)
	2	39661	0.58	0.09	0.04 (0.008)
	3	29652	0.57	0.09	0.04 (0.009)
Survival	1	98936	0.85	0.33	0.02 (0.005)
	2	90397	0.86	0.33	0.02 (0.005)
	3	91634	0.84	0.34	0.02 (0.006)

median, and heterosis and recombination loss coefficients of the cow. When the dependent variable was PRFS, status of the service sire (i.e., stock bull, AI bull < 6 years of age at the time of service, or AI bull >6 years of age at the time of service) was included as a fixed effect while both the service sire and the technician were included as random effects; both random effects were interacted with year of service to account for any temporal differences.

Results

The frequency distribution of the number of calvings, AI services, natural services and pregnancy diagnosis events are illustrated in Figure 1; peak of the respective events were in mid-February, early April, early May, and early October. The mean performance, within each parity, for the different fertility traits is summarised in Table 1. Mean milk yield for parity 1, 2 and 3 animals was 6,057 kg, 6,724 kg, and 7,082 kg in parity 1, 2, and 3, respectively.

There was no obvious trend in fertility performance across the years of calving from 2002 to 2009. Mean CFS varied from 77 days in 2002 to 84 days in 2006; mean CIV varied from 398 days in 2002 to 404 days in 2005. Mean PRFS varied from 0.42 (2004) to 0.46 (2009) while PR42 and CALV42 varied from 0.56 and 0.64 in 2004 to 0.58 (2002) and 0.66 (2006), respectively. Age at first calving decreased linearly ($P<0.01$) by, on average, 5.3 days per year for animals born in 2002 to 2006; 2006 was chosen as the cutoff so that sufficient time to the date of data extraction had been allowed for the full expression of the trait within the time limits imposed during data editing.

Heritability estimates

Heritability estimates from the single trait animal model analyses for all fertility traits are summarised in Table 1. The heritability estimate for AFC was 0.07, and the heritability estimates for the remaining fertility traits varied from 0.01 to 0.07 in primiparae and from 0.01 to 0.04 in pluriparae. The heritability for PRFS was low (0.01 and not different from zero); the genetic correlations estimated with this trait had large associated standard errors and are therefore not shown and this trait is not discussed further. The heritability for survival was 0.02 across all lactations. The heritability for milk yield was 0.27 (SE=0.012), 0.24 (SE=0.013) and 0.24 (SE=0.011) in parity 1, 2, and 3, respectively. The average coefficient of genetic variation for the fertility traits was 8.1% and varied from 3.3% (CIV in parity 3) to 15.3% (PR42 in parity 3).

Correlations within fertility trait, across parities

Phenotypic and genetic correlations across parities for the interval traits and number of services are outlined in Table 2. The genetic correlation for CFS across parities or CIV across parities varied from 0.70 to 0.86; the respective phenotypic correlations were close to zero. Number of services per animal was strongly genetically correlated ($r \geq 0.90$) across parities. Table 3 details the phenotypic and genetic correlations within the binary fertility traits across parities. Calving in the first 42 days of the calving season in parity 1 animals was not genetically correlated with CALV42 in later parity animals. However, the genetic correlations across parities for SR21 and for PR42 were all strong (≥ 0.69).

Correlations among different fertility traits

Calving to first service interval, within parity, was moderately positively genetically correlated (0.54 to 0.75) with CIV (Table 2) and was, in general, moderately

Table 2. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations (standard errors in parentheses) among the interval fertility traits (age at first calving [AFC]; calving to first service interval [CFS]; calving interval [CIV]) and number of services (NS)

Trait†	AFC	CFS1	CFS2	CFS3	CIV1	CIV2	CIV3	NS1	NS2	NS3
AFC		-0.1 (0.006)	-0.02 (0.008)	0.02 (0.011)	0.00 (0.007)	0.03 (0.009)	0.01 (0.012)	0.02 (0.006)	0.03 (0.008)	-0.01 (0.011)
CFS1	0.37 (0.102)		0.04 (0.007)	0.08 (0.009)	0.29 (0.005)	0.02 (0.007)	0.06 (0.010)	-0.09 (0.004)	-0.02 (0.007)	-0.02 (0.009)
CFS2	-0.01 (0.134)	0.80 (0.088)		0.05 (0.008)	-0.07 (0.007)	0.31 (0.006)	0.02 (0.008)	-0.20 (0.007)	-0.10 (0.005)	-0.01 (0.007)
CFS3	0.12 (0.144)	0.70 (0.091)	0.76 (0.097)		0.01 (0.009)	-0.06 (0.008)	0.31 (0.006)	-0.07 (0.009)	-0.22 (0.007)	-0.12 (0.005)
CIV1	0.16 (0.128)	0.63 (0.093)	0.75 (0.102)	0.56 (0.127)		0.04 (0.005)	0.05 (0.007)	0.58 (0.004)	0.04 (0.007)	0.03 (0.009)
CIV2	0.25 (0.123)	0.40 (0.113)	0.75 (0.080)	0.57 (0.112)	0.86 (0.075)		0.04 (0.006)	-0.01 (0.008)	0.58 (0.004)	0.03 (0.008)
CIV3	0.18 (0.141)	0.55 (0.111)	0.51 (0.127)	0.54 (0.119)	0.81 (0.094)	0.84 (0.078)		0.00 (0.010)	-0.01 (0.008)	0.58 (0.004)
NS1	-0.11 (0.145)	-0.16 (0.135)	0.28 (0.157)	0.13 (0.179)	0.50 (0.121)	0.66 (0.121)	0.62 (0.173)		0.07 (0.007)	0.05 (0.009)
NS2	0.05 (0.139)	-0.37 (0.129)	0.15 (0.148)	-0.26 (0.160)	0.47 (0.136)	0.51 (0.110)	0.36 (0.163)	0.98 (0.097)		0.06 (0.007)
NS3	-0.24 (0.148)	-0.11 (0.146)	-0.36 (0.159)	-0.10 (0.159)	0.24 (0.156)	0.48 (0.126)	0.68 (0.117)	0.90 (0.124)	0.99 (0.097)	

†Number at the end of the trait denotes the parity (e.g., CFS1 refers to calving to first service interval in parity 1 animals).

Table 3. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations (standard errors in parentheses) among the binary fertility traits

Trait†‡	CALV421	CALV422	CALV423	SR211	SR212	SR213	PR421	PR422	PR423
CALV421		0.14 (0.007)	0.05 (0.009)	0.22 (0.006)	0.05 (0.008)	0.04 (0.010)	0.49 (0.105)	0.48 (0.123)	0.33 (0.145)
CALV422	0.18 (0.209)		0.23 (0.007)	0.24 (0.007)	0.29 (0.005)	0.12 (0.008)	0.88 (0.088)	0.88 (0.161)	0.83 (0.212)
CALV423	-0.12 (0.166)	0.98 (0.220)		0.09 (0.010)	0.30 (0.007)	0.16 (0.014)	0.41 (0.203)	0.95 (0.078)	0.85 (0.125)
SR211	0.71 (0.080)	0.52 (0.254)	0.42 (0.217)		0.12 (0.008)	0.08 (0.010)	0.91 (0.103)	0.91 (0.178)	0.69 (0.181)
SR212	0.34 (0.120)	0.65 (0.179)	0.58 (0.169)	0.86 (0.201)		0.18 (0.008)	0.94 (0.117)	0.95 (0.099)	0.83 (0.145)
SR213	0.22 (0.175)	0.87 (0.242)	0.79 (0.163)	0.69 (0.255)	0.82 (0.280)		0.99 (0.156)	0.97 (0.117)	0.78 (0.169)
PR421	0.14 (0.006)	0.71 (0.004)	0.25 (0.010)	0.29 (0.005)	0.32 (0.007)	0.15 (0.011)		0.20 (0.008)	0.10 (0.011)
PR422	0.06 (0.008)	0.20 (0.006)	0.72 (0.004)	0.06 (0.008)	0.31 (0.005)	0.38 (0.007)	0.99 (0.108)		0.26 (0.009)
PR423	0.05 (0.011)	0.11 (0.009)	0.24 (0.006)	0.03 (0.011)	0.12 (0.009)	0.34 (0.006)	0.71 (0.168)	0.91 (0.150)	

†Number at the end of the trait denotes the parity (e.g., CALV421 refers to calving in the first 42 days of the calving season for parity 1 animals).
‡CALV42 = calving in the first 42 days of the calving season; SR21 = submission in the first 21 days of the breeding season; PR42 = pregnant in the first 42 days of the breeding season.

negatively correlated with both SR21 (-0.68 to -0.29; Table 4) and PR42 (-0.36 to -0.14; Table 4); correlations with NS (Table 2) and CALV42 (Table 4) were not consistent within parity. Calving interval was moderately positively correlated (0.24 to 0.68) with NS. Irrespective of parity, the genetic correlations between CIV and CALV42, SR21 and PR42 were all negative. The genetic correlations between CALV42, SR21 and PR42 were all positive (Table 3).

Correlations between fertility and both survival and milk yield

Table 5 outlines the genetic correlations between fertility and both survival and milk yield. The genetic correlations, within parity, between milk yield and survival were -0.22 (SE=0.108), -0.07 (SE=0.138) and -0.05 (SE=0.121) in parity 1, 2 and 3, respectively. Superior fertility, almost irrespective of the fertility trait, including earlier age at first calving, was associated with improved survival. With the exception of the correlation between CFS in parity 3 and survival in parity 1 (0.17; SE=0.17), the genetic correlations between survival and the interval traits varied from -0.77 (CIV in parity 2 and survival in parity 1) to -0.24 (CIV in parity 3 and survival in parity 1). Genetic correlations between NS and survival varied from -0.74 (NS in parity 1 and survival in parity 2) to -0.10 (NS in parity 3 and survival in parity 1). Genetic correlations between the binary traits and survival varied from 0.05 (CALV42 in parity 1 and survival in parity 1) to 0.80 (PR42 in parity 3 and survival in parity 3). In general the correlations between PR42 and survival were stronger than the correlations between either CALV42 or SR21 with survival.

Milk yield was antagonistically genetically correlated with fertility in primiparae

Table 4. Genetic correlations (standard errors in parentheses) between the interval, count and binary fertility traits

Trait[†‡]	AFC	CFS1	CFS2	CFS3	CIV1	CIV2	CIV3	NS1	NS2	NS3
CALV421	-0.40 (0.077)	0.38 (0.072)	0.04 (0.106)	-0.08 (0.115)	-0.11 (0.104)	-0.45 (0.087)	-0.03 (0.119)	0.14 (0.12)	-0.22 (0.112)	-0.20 (0.117)
CALV422	-0.36 (0.286)	-0.40 (0.222)	-0.26 (0.224)	0.39 (0.241)	-0.43 (0.211)	-0.68 (0.163)	-0.76 (0.193)	-0.33 (0.230)	-0.02 (0.147)	-0.76 (0.215)
CALV423	-0.28 (0.196)	-0.52 (0.155)	-0.34 (0.180)	0.19 (0.172)	-0.43 (0.184)	-0.36 (0.162)	-0.57 (0.161)	-0.30 (0.216)	-0.05 (0.207)	-0.11 (0.206)
SR211	-0.36 (0.153)	-0.64 (0.121)	-0.63 (0.164)	-0.39 (0.185)	-0.74 (0.151)	-0.63 (0.157)	-0.46 (0.184)	0.04 (0.204)	-0.21 (0.083)	-0.07 (0.098)
SR212	-0.24 (0.151)	-0.78 (0.113)	-0.68 (0.123)	-0.41 (0.159)	-0.60 (0.14)	-0.63 (0.132)	-0.65 (0.141)	-0.33 (0.179)	-0.24 (0.143)	-0.16 (0.157)
SR213	-0.12 (0.205)	-0.82 (0.163)	-0.61 (0.206)	-0.29 (0.209)	-0.28 (0.244)	-0.74 (0.140)	-0.70 (0.184)	-0.36 (0.147)	-0.40 (0.093)	-0.26 (0.102)
PR421	-0.41 (0.129)	-0.32 (0.135)	-0.28 (0.183)	-0.40 (0.167)	-0.68 (0.118)	-0.84 (0.101)	-0.80 (0.123)	-0.66 (0.103)	-0.53 (0.187)	-0.56 (0.200)
PR422	-0.16 (0.167)	-0.46 (0.157)	-0.36 (0.172)	-0.08 (0.202)	-0.81 (0.123)	-0.77 (0.098)	-0.83 (0.132)	-0.60 (0.150)	-0.51 (0.148)	-0.68 (0.154)
PR423	0.05 (0.177)	-0.48 (0.162)	-0.26 (0.187)	-0.14 (0.188)	-0.39 (0.201)	-0.80 (0.110)	-0.79 (0.115)	-0.39 (0.171)	-0.55 (0.176)	-0.70 (0.123)

[†]Number at the end of the trait denotes the parity (e.g., CFS1 refers to calving to first service interval in parity 1 animals).
[‡]AFC = age at first calving; CFS = calving to first service interval; CIV = calving interval; NS = number of services; CALV42 = calving in the first 42 days of the calving season; SR21 = submission in the first 21 days of the breeding season; PR42 = pregnant in the first 42 days of the breeding season.

Table 5. Genetic correlations (standard errors in parentheses) between fertility and both survival in parity 1 to 3 and milk yield (Milk) in parity 1 to 3

Trait[†]	Survival1	Survival2	Survival3	Milk1	Milk2	Milk3
AFC	-0.23 (0.149)	-0.43 (0.143)	-0.50 (0.128)	0.14 (0.075)	0.13 (0.076)	-0.06 (0.084)
CFS1	-0.36 (0.143)	-0.47 (0.143)	-0.26 (0.142)	0.29 (0.070)	0.15 (0.074)	0.21 (0.079)
CFS2	-0.39 (0.164)	-0.59 (0.131)	-0.30 (0.151)	0.29 (0.092)	0.38 (0.077)	0.37 (0.084)
CFS3	0.17 (0.174)	-0.29 (0.175)	-0.31 (0.156)	0.24 (0.097)	0.08 (0.093)	0.05 (0.097)
CIV1	-0.74 (0.107)	-0.74 (0.124)	-0.49 (0.144)	0.44 (0.069)	0.27 (0.079)	0.29 (0.085)
CIV2	-0.77 (0.105)	-0.73 (0.114)	-0.69 (0.106)	0.42 (0.073)	0.40 (0.071)	0.48 (0.071)
CIV3	-0.24 (0.167)	-0.61 (0.142)	-0.66 (0.112)	0.43 (0.093)	0.39 (0.087)	0.43 (0.083)
NS1	-0.32 (0.176)	-0.74 (0.156)	-0.39 (0.190)	0.38 (0.096)	0.20 (0.106)	0.23 (0.116)
NS2	-0.27 (0.183)	-0.34 (0.193)	-0.55 (0.162)	0.14 (0.102)	0.14 (0.101)	0.14 (0.106)
NS3	-0.10 (0.188)	-0.26 (0.196)	-0.48 (0.152)	0.29 (0.102)	0.19 (0.100)	0.40 (0.095)
CALV421	0.05 (0.133)	0.08 (0.149)	0.17 (0.128)	0.09 (0.055)	-0.01 (0.057)	0.12 (0.062)
CALV422	0.34 (0.252)	0.06 (0.271)	0.61 (0.201)	-0.25 (0.167)	-0.11 (0.164)	-0.08 (0.162)
CALV423	0.38 (0.199)	0.53 (0.186)	0.29 (0.195)	-0.18 (0.133)	-0.09 (0.128)	-0.12 (0.134)
SR211	0.15 (0.218)	0.27 (0.221)	0.12 (0.211)	0.03 (0.130)	0.07 (0.129)	-0.10 (0.136)
SR212	0.48 (0.173)	0.34 (0.190)	0.28 (0.178)	-0.39 (0.108)	-0.29 (0.109)	-0.33 (0.113)
SR213	0.65 (0.195)	0.75 (0.187)	0.74 (0.176)	-0.33 (0.151)	-0.27 (0.149)	-0.18 (0.153)
PR421	0.63 (0.158)	0.67 (0.157)	0.20 (0.193)	-0.03 (0.107)	-0.15 (0.106)	-0.13 (0.118)
PR422	0.67 (0.145)	0.53 (0.182)	0.43 (0.176)	-0.37 (0.116)	-0.46 (0.114)	-0.50 (0.116)
PR423	0.33 (0.215)	0.60 (0.205)	0.80 (0.123)	-0.34 (0.137)	-0.30 (0.131)	-0.27 (0.121)

[†]Number at the end of the trait denotes the parity (e.g., CFS1 refers to calving to first service interval in parity 1 animals).
[‡]AFC = age at first calving; CFS = calving to first service interval; CIV = calving interval; NS = number of services; CALV42 = calving in the first 42 days of the calving season; SR21 = submission in the first 21 days of the breeding season; PR42 = pregnant in the first 42 days of the breeding season.

and pluriparae with the exception of both CALV42 and SR21 in parity 1 animals, where the correlation was favourable albeit close to zero.

Discussion

Fundamental to profitable seasonal calving production systems are cows that return to service early post-calving and subsequently conceive and maintain pregnancy to calve early in the following calving season. To date, genetic evaluations for fertility in Ireland were based on CIV, due mainly to a lack of routine information on services. The objective of the present study was to undertake the first phenotypic and genetic analysis of service and pregnancy diagnosis data now collected nationally on a routine basis in Ireland and to evaluate the feasibility of selecting on different measures of fertility.

Mean fertility performance in the present study, based on field data, is below the targets set for seasonal calving herds (O'Farrell 1994). The weighted average across parities for CFS (79 days) is below the target, as is the weighted average of 398 days for CIV which is longer than the required 365 days to maintain a strict seasonal calving system. However, both traits are positively skewed and the weighted median, across parities, for CFS and CIV was 77 and 375, respectively. Furthermore, the average PRFS of 0.45 is below the target of 0.60 and is also slightly lower than the estimate of 0.49 reported from a large scale research study undertaken on 78 Irish commercial herds with accurately recorded fertility data (Berry *et al*. 2003). The higher proportion of first parity animals calving in the first 42 days of the calving season is because these animals were served as heifers and synchronisation may have been used in the heifers on some farms. Mean fertility performance in the sample population used in this study is inferior to performance reported by Grosshans *et al*. (1997) in New Zealand, albeit based on data many years earlier than that used in the present study but is nonetheless similar to fertility performance reported from Australia (Haile-Mariam *et al*. 2003)

There is a general consensus based on the plethora of international studies (Pryce and Veerkamp 2001; Wall *et al*. 2003), albeit mainly in confinement or year-round calving systems of milk production, that traditional measures of fertility are lowly heritable. Fewer heritability estimates, however, have been documented for traits pertinent to seasonal calving herds where one could potentially expect a greater expression of genetic differences among animals because of demands to conceive within a strict period post-calving. Grosshans *et al*. (1997) using data on Holstein and Jersey cows in New Zealand reported heritability estimates of pregnant in the first 21 and 42 days of the breeding season of between 0.03 and 0.04 in first and second lactation animals; Evans *et al*. (2002) using data on 3,087 Irish Holstein-Friesian cows reported respective heritability estimates of 0.00 and 0.02. Similarly, Haile-Mariam *et al*. (2003) reported a heritability of 0.06 for PR42 in Australian Holstein-Friesian cattle. Although not always consistent within and across studies, including the present study, there does seem to be a tendency for fertility traits related to return to service (e.g., interval from calving/start of the breeding season to first service, SR) to be more heritable than traits associated with conception rate or pregnancy rate irrespective of the production system (Grosshans *et al*. 1997; Evans *et al*. 2002; Haile-Mariam *et al*. 2003; Pryce *et al*. 1997; Wall *et al*. 2003). Differences between traits, other than being attributable to true genetic differences, may be influenced by potentially greater inaccuracies associated with the correct definition of conception or pregnancy status as well as the binary nature of some of the conception or pregnancy related traits. Inappropriate statistical modelling of these complex phenotypes may also contribute to low heritability estimates owing to, for example, systematic environmental effects not being captured by the fixed component of the statistical model entering the residual term. Nonetheless, heritability estimates for fertility traits in other studies, agreeing with the estimates in the present study, do confirm that, irrespective of the system of milk production, traditional measures of fertility are lowly heritable.

The coefficient of genetic variation in fertility in the present study (3.3% to 15.3%) agrees with the existence of considerable variation in fertility reported by others or calculated from the statistics reported by others (Wall *et al*. 2003; Dematawewa and Berger 1998; Berry *et al*. 2003). These estimates of genetic variation are similar to estimates obtained in the same studies for milk yield traits; the coefficient of genetic variation for milk yield in the present study varied from 6.6% to 6.8%. This clearly signifies that, if accurate estimates of genetic merit for fertility can be obtained, then rapid genetic gain in fertility is possible, although this will also be dependent on the genetic correlations with other traits included in the breeding goal as well as the relative selection pressure placed on the traits. Increasing the accuracy of estimated breeding values for low heritability traits is now a possibility with the exploitation of genomic selection (Meuwissen *et al*. 2001). However, key to the success of any genomic selection breeding program is access to a large reference population with accurately defined phenotypes for the estimation of genetic marker effects.

Comparison of different fertility traits

The choice of which traits to include in a breeding goal is a function not only of the genetic variation present and time duration required to measure the phenotype or correlated trait, but also the heritability of the trait as well as the quantity of data available from which to estimate breeding values. The goal trait currently included in the Irish total merit index, the Economic Breeding Index (Berry *et al*. 2007) to reflect fertility performance is CIV (Olori *et al*. 2002). However, only animals that re-calve will have an actual phenotype for CIV and therefore survival to the subsequent lactation is included in the multi-trait genetic evaluation to account for this, as well as being included itself in the Economic Breeding Index with an economic weight (Berry *et al*. 2007). Information on CFS, on the other hand, will be available earlier post-calving and will be available on all animals served using AI by field technicians, irrespective of whether or not the animal re-calved. Inclusion in a multi-trait genetic evaluation with fertility will account for selection bias. However, there is a tendency for farmers undertaking their own AI to only record the last insemination; this can possibly be overcome, however, by education and these farms were excluded from this study. Furthermore, CFS will not generally be available from herds that operate strictly natural mating. However, more importantly, CFS does not take cognisance of the ability of the animal to become pregnant; within parity, 29 to 56% of the genetic variation in CIV was attributable to genetic differences in CFS. A similar conclusion was evident for SR21. Although presentation for service during the start of the breeding season is important in seasonal breeding herds, SR21 does not reflect the ability of the animal to conceive.

In the present study, no significant genetic variation in PRFS was observed; coupled with the short AI breeding season, PRFS or similar traits (56-day non-return rate), may not be suitable fertility traits for seasonal breeding herds using natural mating. The lack of significant genetic variation in PRFS may reflect the inadequacy of the data used in the present study to truly identify genetic variation in this trait. Nonetheless, phenotypically at least, the association between CFS and PRFS is non-linear, with a favourable association up to 238 days post-calving and an unfavourable association thereafter (Berry, Evans and McParland 2011). Therefore, selection on shorter CFS without cognisance of pregnancy rate is not recommended although, on average, shorter CFS is genetically associated with shorter CIV. Nonetheless, separating CIV into its individual components of both CFS and pregnancy rate, facilitates better adjustment for systematic environmental effects (e.g., service sire and AI technician effects on pregnancy rate; Berry *et al*. 2011) in the genetic evaluation model and may therefore be superior than selection on CIV itself.

Pregnant in the first 42 days of the breeding season encompasses both the ability of the animal to return to cyclicity and also to become pregnant. However, without pregnancy diagnoses being recorded, confirmation of a positive pregnancy is not available until the subsequent calving, if recorded and therefore this trait also suffers from similar disadvantages to CIV.

Whether or not a cow calves within a given period relative to the start of the herd calving season is arguably one of the most important traits in a seasonal calving herd. It is a legal requirement to record calving dates in Ireland so data are routinely available. However, the heritability of CALV42 was low (0.01 to 0.02) and in some herds it was not possible to identify the start of the calving season and therefore data were omitted. Furthermore, CALV42 is influenced by the direct genetic effect for gestation length of the sire which may not always be recorded especially for natural mating bulls.

Finally, the genetic correlations between all fertility traits were not unity suggesting that to improve overall fertility, cognisance of several traits should be considered.

Genetic (co)variances with survival and milk yield

Across all fertility traits and parities, genetic merit for fertility explained between 0.2% (CALV42 in parity 1 and survival in parity 1) and 64.5% (PR42 in parity 3 and survival in parity 3) of the genetic variance in survival; the average was 23%. Previous studies from confinement or year-round calving systems reported that fertility accounted for, on average, 5.3% (Dematawewa and Berger 1998) to 6% (Roxström and Strandberg 2002) of the genetic variance in survival related traits, although in some studies (Dematawewa and Berger 1998) the reported correlations suggested that survival was actually genetically associated with inferior fertility. The proportion of variation in survival attributable to genetic differences in fertility in seasonal calving herds has been documented to be, on average, 8.7% (Haile-Mariam *et al*. 2003). Comparison of correlations between fertility and survival in previous studies with the present study suggest a greater genetic contribution of fertility to whether or not a cow is retained in Irish seasonal calving herds.

The generally antagonistic genetic correlations, within parity, between fertility and milk production corroborate most previous studies (Berry *et al*. 2003; Grosshans *et al*. 2007; Pryce *et al*. 1997; Dematawewa and Berger 1998) clearly indicating that selection for milk production, with no cognisance of non-production traits, will result in a decline in genetic merit for fertility. Genetic trends from such correlated responses to selection on past breeding programs which aggressively selected for high milk output has been documented elsewhere (Royal *et al*. 2002).

Conclusions

Heritability estimates for fertility traits in the present study of seasonal calving Holstein-Friesian cows were low (i.e., ≤0.07) corroborating previous reports from seasonal calving and year-round calving systems of milk production. The fertility traits defined in the present study, pertinent to seasonal calving and seasonal breeding production systems, each have their own advantages and disadvantages and no one trait can adequately describe the overall fertility performance of an animal. Therefore, several traits should be taken into account in national genetic evaluations for fertility, especially given the moderate to strong correlations between fertility and survival identified in the present study which itself is also an economically important trait.

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