



Additive genetic, non-additive genetic and permanent environmental effects for female reproductive performance in seasonal calving dairy females

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Abstract

Excellent reproductive performance (i.e. 365-day calving interval) is paramount to herd profit in seasonal-calving dairy systems. Reproductive targets are currently not being achieved in Irish dairy herds. Furthermore, most research on the genetics of reproductive performance in dairy cattle has focused primarily on lactating cows and relatively few studies have attempted to quantify the genetic contribution to differences in reproductive performance in nulliparae. The objective of the present study was to estimate the contribution of both the additive and non-additive genetic components, as well as the permanent environmental component, to phenotypic variation in the reproductive traits in nulliparous, primiparous and multiparous seasonal-calving dairy females. Reproductive phenotypes were available on up to 202,525 dairy females. Variance components were estimated using (repeatability where appropriate) linear animal mixed models; fixed effects included in the mixed models were contemporary group, parity (where appropriate), breed proportion, inter-breed specific heterosis coefficients and inter-breed specific recombination loss coefficients. Heritability of the reproductive traits ranged from 0.004 (pregnancy rate to first service) to 0.17 (age at first service in nulliparae), while repeatability estimates for the reproductive traits in cows ranged from 0.01 (calving interval) to 0.11 (pregnant in the first 42 days of the breeding season). Breed-specific heterosis regression coefficients suggest that, relative to the parental mean, a first-cross Holstein–Jersey crossbred was almost 7 days younger at first calving, had a 9-day shorter calving interval, a 6 percentage unit greater pregnancy rate in the first 42 days of the breeding season and a 3 percentage unit greater survival rate to next lactation. Heifer calving rate traits were strongly genetically correlated with age at first calving (–0.97 to –0.66) and calving rate in the first 42 days of the calving season for first parity cows (0.77 to 0.56), but genetic correlations with other cow reproductive traits were weak and inconsistent. Calving interval was strongly genetically correlated with the majority of the cow traits; 56%, 40%, and 92% of the genetic variation in calving interval was explained by calving to the first service interval, number of services and pregnant in the first 42 days of the breeding season, respectively. Permanent environmental correlations between the reproductive performance traits were generally moderate to strong. The existence of contributions from non-additive genetic and permanent environmental effects to phenotypic differences among cows suggests the usefulness of such information to rank cows on future expected performance; this was evidenced by a stronger correlation with future reproductive performance for an individual cow index that combined additive genetic, non-additive genetic and permanent environmental effects compared to an index based solely on additive genetic effects (i.e. estimated breeding values).

Keywords

heritability • heterosis • permanent environment • recombination

Introduction

There is a general consensus that strong selection for milk production has resulted in a deterioration in reproductive performance in lactating dairy cows due to the now well-accepted antagonistic genetic correlations between milk yield and reproductive performance (Veerkamp and Beerda, 2007; Berry *et al.*, 2014). This deterioration in reproductive performance has motivated the broadening of dairy cattle breeding goals internationally to include functional traits (Miglior *et al.*, 2005). Most research pertaining to the genetics of reproductive performance in dairy cattle has focused primarily on lactating cows (Royal *et al.*, 2002; Kadarmideen

et al., 2003; Cutullic *et al.*, 2012). Relatively few studies have attempted to quantify the genetic contribution to reproductive performance in nulliparous heifers (Raheja *et al.*, 1989; Pryce *et al.*, 2002; Kuhn *et al.*, 2006). Also lacking is information on the genetic relationship between heifer and cow reproductive performance and its potential value to enhance reproductive performance (Tiezzi *et al.*, 2012). In a UK study, Wathes *et al.*, (2008) reported that perinatal mortality accounted for 7.9% of dairy calves born, while a further 6.7% of heifers died during the rearing stage, before even reaching the breeding age of 15 months. Of the remaining heifers, 2.3% failed to

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conceive and 3.3% died or were culled due to infertility between 15 months of age and expected calving age. Of the heifers that failed to conceive at 15 months of age, some were re-inseminated later in the year and subsequently calved for the first time older than 30 months of age (Wathes *et al.*, 2008). Although management also affects reproductive performance, some of the results observed by Wathes *et al.*, (2008) were also likely due to genetic effects. Therefore, in addition to achieving optimal conception rate in nulliparous heifers, the loss of potential replacement heifers through mortality, failure to conceive or due to abortions should be accounted for in national genetic evaluations for reproductive performance.

Most study populations used in the estimation of variance components for reproductive performance traits consist of purebred cattle (Wall *et al.*, 2003; Jamrozik *et al.*, 2005; Liu *et al.*, 2008) and therefore heterosis and recombination loss estimates for reproductive performance are scarce, especially breed-specific heterosis estimates (Wall *et al.*, 2005). The low heritability of traditional measures of reproductive performance traits (Berry *et al.*, 2014) manifests itself as generally low reliability of estimates of genetic merit for cows. Incorporating additional effects, such as permanent environmental effects and other non-additive genetic effects, into decision support tools (e.g., some form of performance index) could provide a better alignment to the expected reproductive performance and rank females to aid in culling decisions based on expected future performance. Repeatability estimates of reproductive performance traits are generally lacking (Pryce *et al.*, 1999; Philipsson and Lindhé, 2003; Wall *et al.*, 2003; Liu *et al.*, 2008), especially in seasonal-calving dairy herds.

The objective of the present study was to estimate genetic (both additive and non-additive genetic) and environmental variance components for a range of reproductive performance traits in nulliparous, primiparous and multiparous seasonal-calving dairy females. The results from this study will be useful to inform the potential impact of improving reproductive performance in Irish dairy cattle, through genetic selection if sufficient genetic variation exists in these traits, but also to determine the additional sources of variation that contribute to the phenotypic performance of reproductive performance traits. A further exploratory aim of the study was to examine the possibility of developing a reproductive index with the view to rank dairy females more aligned to their expected phenotypic reproductive performance.

Materials and Methods

Data

Data on a range of animal-level events including date of calving, information on services, pregnancy diagnoses, slaughter and

between herd animal movements (including death), from the years 2006 to 2012 (both years inclusive), were available from the Irish Cattle Breeding Federation (ICBF) database. Pedigree information on all animals including breed proportion was also available. Only records from animals with at least 87.5% known dairy breed proportion were retained. Dairy breeds considered in this study included Holstein (HO), Friesian (FR), Jersey (JE) and Montbéliarde (MO); all remaining dairy breeds were excluded from the analysis because of their low incidence in the Irish population. Several reproductive phenotypes in heifers and cows were generated, many of which have been described in detail previously by Berry *et al.*, (2013). The data available consisted of up to 2,800,318 lactations from 1,105,674 dairy cows in 19,397 dairy herds.

Nulliparous reproductive traits

Age at first service (AFS) was defined as the age, in days, when a nulliparous heifer was first served. Only AFS records between 365 days (i.e. 1 year) and 913 days (i.e. 2.5 years) were used in the analysis. Some Irish herds use synchronisation protocols in heifer fertility management, which may bias AFS. Therefore, all data from herd-years with at least 10 heifers, where more than half of heifers were recorded as being inseminated in a single day, were discarded. Age at first calving (AFC) was defined as the age, in days, when the animal calved for the first time. Only AFC records between 550 and 1250 days were retained for subsequent analysis. A binary trait, heifer calving rate (HCR), was defined as calved (HCR=1) or not (HCR=0) at least once during her lifetime. Heifers that died or were slaughtered without a recorded calving date were assigned zero for HCR. Similarly, heifers that were sold at an age older than 12 months without a subsequent recorded calving date were assigned a value of zero. Heifers sold prior to 12 months of age were coded as missing. Heifers with no calving, sale, slaughter or death data, born within 38 months of the date of data extraction from the national database, were also coded as missing. An additional binary trait, HCR26, was defined as HCR with an age limit of 26 months for the first calving event to have occurred. Heifers that calved for the first time >26 months of age were coded as zero for HCR26, or were coded as missing for heifers born within 26 months of the date of data extraction without a recorded calving, sale, slaughter or death date. All other information relating to the HCR26 phenotypic value remained the same as the previously described HCR. An identical approach was used for the definition of HCR38, where 38 months of age was used as the age threshold for the first calving event.

Cow reproductive traits

Calving to first service interval (CFS) was defined, within lactation, as the number of days between calving and first

insemination. Only CFS records between 10 and 250 days were retained. Calving interval (CIV) was defined as the number of days between two successive calving dates. Only CIV records >300 days were retained. Where a CFS record <150 days existed (an attempt was made by the farmer to retain the cow within an annual calving cycle), a CIV up to 800 days was permitted within the analysis; otherwise, a CIV upper threshold restriction of 600 days was imposed.

Submission in the first 21 days of the breeding season (SR21) was defined as whether a cow was inseminated (SR21=1) or not (SR21=0) in the first 21 days of the herd's breeding season, irrespective of calving date. Only cow data were used in the definition of the breeding season. Breeding season start date was defined separately per herd, as the date initiating a period where at least 5 cows were inseminated within the next 14 days. The breeding season end date was defined as the date with no recorded insemination in the subsequent 10 days, or the date where the number of days between the next three consecutive inseminations was more than 21 days apart. Only breeding seasons with at least 20 inseminations and between 5 and 20 weeks in length were considered. Cows served before the start of the breeding season were set to missing for SR21. Number of services (NS) was defined as the number of inseminations a cow received during the breeding season. Number of services >10 were set to 10.

Pregnant in the first 42 days of the breeding season (PR42) was defined as whether a cow became pregnant (PR42=1) or not (PR42=0) in the first 42 days of the breeding season. This trait was not defined for nulliparous heifers and only data from herds using some AI, and where the AI breeding season was at least 42 days in length, were considered. Cows with a positive pregnancy diagnosis, confirming pregnancy during the first 42 days of breeding season, were recorded as pregnant for PR42. Additionally, cows with a subsequent calving date record, which allowed for a biologically plausible gestation length (between 265 and 295 days for females mated to HO×FR sires or between 265 and 300 days for females mated to other breed sires (Norman *et al.*, 2009)), were recorded as pregnant for PR42. Cows were coded as not pregnant for PR42 if a service date record was recorded after day 42 of the breeding season or where a calving date >248 days from the start of the previous breeding season was recorded. Where a PR42 record did not already exist, PR42 was set to missing for cows served within 30 days of the AI breeding end date or for cows that were culled within 30 days of the last service.

Pregnancy rate to first service (PRFS) was defined as pregnant to first service (PRFS=1) or not (PRFS=0). Cows were recorded as PRFS=0 where the number of services was >1. PRFS was set to missing for cows where the first service was recorded within 30 days of the end of the AI

breeding season or within 30 days of being culled and no second service existed. Pregnancy diagnosis data were used to confirm PRFS. Cows were coded as pregnant for PRFS where a subsequent calving date record was available that could confirm pregnancy to the first service-taking cognisance of gestation length. The gestation length range was as outlined in the definition for PR42.

Calving in the first 42 days (CR42) of the herd calving season was defined as whether a cow calved (CR42=1) or not (CR42=0) in the first 42 days of the calving season. The calving season was defined separately for primiparous and multiparous cows. The start date of the calving season was defined as the first calving date within a herd, where at least five cows calved within the subsequent 14-day period. Calving season end date was defined as the last calving date in a herd with no subsequent calving events occurring in the next 30 days for primiparous cows or the next 21 days for multiparous cows. Cows with a recorded calving date within 14 days before the start of the calving season were coded as having calved within the first 42 days of the calving season, to account for premature births and short gestations. Only calving seasons 35 and 200 days in length in herds of >20 multiparous cows or in herds of >6 for primiparous cows, respectively, were retained.

The binary trait of survival (SURV) was defined as whether a cow survived to next lactation (SURV=1) or not (SURV=0). Cows with a subsequent calving date were coded as having survived (SURV=1). Cows without a recorded calving date within 800 days of the last recorded calving date for that herd were assumed not to have survived (SURV=0). If a slaughter date or death date was recorded, then the cow was assumed not to have survived that lactation (SURV=0). Cows were coded as missing for SURV if the last recorded calving date of the cow was within 800 days of the date of data extraction and a death date or slaughter date was not available.

Age at first service, CFS, SR21, NS, PRFS and PR42 records from herd-years where >80% of animals were recorded as having only one service record were discarded due to the risk of incomplete insemination records.

Contemporary groups

Contemporary groups were formed based on the procedures outlined in detail by Berry *et al.*, (2013). The algorithm grouped animals, within herd, based on proximity of date of the event under investigation. For nulliparae traits (AFS, AFC, HCR, HCR26, HCR38) and primiparae CR42, the contemporary group of herd-year-season of birth was generated, using an algorithm to group animals in close proximity for date of birth and within the same herd of birth. Nulliparous heifers purchased into a herd from 12 months of age were included in the contemporary group of the herd of purchase and date

of birth for the heifer calving rate traits (HCR, HCR26 and HCR38). Contemporary group of herd-year-season of calving was generated for each multiparous trait. The algorithm grouped cows, within herd, on proximity in calving date. For all traits, only contemporary groups with five or more records were retained. A random sample of contemporary groups was chosen within trait and from herd-years where at least 10% of the herd were crossbred to result in a dataset with, where possible, approximately 100,000 records per trait. The number of records included in the analyses for each trait is detailed in Table 1.

Heterosis and recombination loss coefficients

Breed combination-specific heterosis and recombination loss coefficients were calculated as per Dickerson (1973):

$$\text{HETEROSIS}_{ij} = \sum_{i=1}^2 \alpha_{S_i} \cdot \alpha_{D_j}$$

$$\text{RECOMBINATION}_{ij} = \sum_{\substack{X \in (S,D) \\ i=1 \\ j \neq i}}^2 \alpha_{X_i} \cdot \alpha_{X_j}$$

where HETEROSIS_{ij} is the heterosis coefficient between the *i*-th and *j*-th breed-specific combination, RECOMBINATION_{ij} is the recombination loss coefficient between the *i*-th and

j-th breed-specific combination, α_{S_i} and α_{S_j} are the proportion of breed *i* and *j* in the sire, respectively, and α_{D_i} and α_{D_j} are the proportion of breed *i* and *j* in the dam, respectively. The breeds considered in this study included HO, FR, JE and MO; breed-specific non-additive effects were estimated for each combination (heterosis effects and recombination loss effects for HO×FR, HO×JE, HO×MO, FR×JE, FR×MO, JE×MO).

Statistical analysis

Variance components for each reproductive performance trait were estimated using linear animal mixed models; for traits of multiparous cows, a repeatability linear animal mixed model was used, represented as:

$$y = Xb + Za + Wpe + e$$

where *y* is the vector of observed phenotypes. *X*, *Z*, *W* relate to the incidence matrices relating to *y* to *b*, *a* and *pe*, respectively; *b* is the fixed effects, *a* is the animal genetic effect, *pe* is the permanent environment effect and *e* is the random residual effect. The fixed effects included in the model were contemporary group, parity (where relevant), breed, breed-specific heterosis coefficient and breed-specific recombination loss coefficient. Holstein breed proportion was not included in the model to avoid linear dependencies. The random effects included in the model were additive genetic effects and random permanent environment effects.

Prediction of cow reproductive performance

The usefulness of incorporating additive genetic effects, as well as non-additive genetic and permanent

Table 1. Number of records (N), mean, genetic standard deviation (σ_g), heritability (h²) and repeatability (t) for reproductive performance traits.

	N	Mean	σ _g	h ²	t
Age at first calving [§] (days)	70377	733	4.85	0.01 (0.003)	
Age at first service [§] (days)	64689	446	14.65	0.17 (0.015)	
Heifer calving rate	82436	0.77	0.07	0.04 (0.007)	
Heifer calving rate at 26 months	82620	0.68	0.07	0.04 (0.006)	
Heifer calving rate at 38 months	82625	0.76	0.06	0.04 (0.006)	
Calving rate in first 42 days calving season for primiparae	46403	0.84	0.03	0.006 (0.003)	
Calving to first service (days)	142344	76	2.22	0.02 (0.003)	0.04 (0.004)
Calving interval [§] (days)	141942	369	6.46	0.01 (0.002)	0.01 (0.004)
Calving rate in first 42 days calving season for multiparae	97963	0.70	0.02	0.006 (0.002)	0.06 (0.005)
Number of services	142344	1.56	0.08	0.01 (0.002)	0.05 (0.004)
Pregnancy rate in first 42 days breeding season	115858	0.69	0.06	0.02 (0.003)	0.11 (0.005)
Pregnancy rate to first service	116665	0.52	0.05	0.004 (0.005)	0.01 (0.006)
Submission rate in first 21 days breeding season	126753	0.76	0.06	0.03 (0.004)	0.09 (0.004)
Survival rate	202525	0.86	0.04	0.02 (0.002)	0.02 (0.002)

[§]Median presented instead of mean.

environmental components, into an index to predict future cow reproductive performance was investigated. To do so, alternative approaches were used to estimate the next lactation reproductive performance in multiparous cows. The multiparous reproductive traits considered were CFS, CIV, SR21, NS, PRFS, PR42 and SURV. The dataset was separated into a calibration (years 2006 to 2010) and a validation (year = 2011) dataset; the calibration and validation dataset included 166,596 and 59,642 records, respectively. The predictor variable and variable to be predicted were both defined within a mixed model framework. Fixed effects included in the model were contemporary group, parity, breed, breed-specific heterosis coefficients and breed-specific recombination loss coefficients. Holstein breed proportion was not included in the model to avoid linear dependencies. Animal was included as the random effect. The gold standard validation phenotype to be predicted was generated from the mixed model applied to the validation dataset and was defined as the sum of the animal effects (no relationships among animals considered), fixed effects (except for contemporary group solutions) and the residual error solution. Three alternative predictor variables from the calibration dataset were considered: (1) adjusted phenotype, (2) estimated breeding value (EBV) and (3) reproductive performance index. All were estimated from the applied mixed model. The adjusted phenotype was as described for the validation dataset and was the sum of the animal effects (no relationships among animals considered), fixed effects (except for contemporary group solutions) and the residual error solution. The EBV predictor variable was the sum of the EBV from the mixed model and the relevant breed effects; in this model, the animal component was decomposed into the direct genetic effects (including relationships) and the permanent environmental effects. The reproductive performance index per cow was derived from the mixed model with the animal component decomposed into the direct genetic effect (based on the numerator relationship matrix) and the permanent environmental effects, and the reproductive performance index was calculated as the sum of the additive genetic effects, permanent environmental effects, breed effects, breed-specific heterosis effects and breed-specific recombination loss effects.

Results

Summary statistics for the reproductive performance of the animals in the study are in Table 1. Fifty-two per cent of cows were pregnant to first service, with 69% of cows establishing pregnancy in the first 6 weeks of the breeding season. Calving interval was positively skewed with a median of 369 days. Only 68% of heifers calved by 26 months of age, with a further 8 percentage units (i.e. 76%) calving by 38 months of age. In total, 23% of heifer calves born, never calved in their lifetime. Table 2 provides the breed structure of the dataset. Over 40% of the cows in the present study were HO×FR and 13% were HO×JE.

Breed and heterosis effects

Breed effect estimates, expressed as a deviation from HO, are in Table 3. Relative to the HO, MO females were older ($P<0.001$) at first service (21 days) and first calving (37 days), as well as, on average, displaying a 13 and 3 percentage unit lower ($P<0.001$) calving rate in the first 6 weeks of the calving season in primiparous and multiparous cows, respectively. Relative to the HO, 13 percentage units less ($P<0.001$) MO heifers calved by 26 months of age. For JE females, CFS was over 2.5 days shorter ($P<0.001$), SR21 was 7 percentage units greater ($P<0.001$) and SURV was 3 percentage units greater ($P<0.001$) relative to HO females.

Breed-specific heterosis and recombination loss estimates are in Tables 4 and 5, respectively. Age of first calving was 28 days earlier ($P<0.001$), CIV was 9.5 days shorter ($P<0.001$) and SURV was 4 percentage units greater ($P<0.001$), on average, for an F₁ HO×MO crossbred female compared to the respective mean performance of the parental breeds. Breed-specific heterosis estimates for all reproductive performance traits, except CR42, HCR and HCR38, were all favourable and significantly different from zero for the HO×JE cross. The majority of breed-specific recombination loss solutions for the reproductive traits were not different from zero. The most significant recombination loss estimates were for SURV. Survival rate was an additional 2 percentage units greater ($P<0.05$) for the HO×JE and was reduced ($P<0.05$) by 4.5 percentage units for the FR×JE at 50% recombination loss.

Table 2. Breed structure percentages for primary breed and secondary breeds within Holstein, Friesian, Jersey and Montbéliarde (purebreds along the diagonal) for the dataset used in the current study.

Secondary breed	Holstein	Friesian	Jersey	Montbéliarde
Holstein	4.81	8.94	12.81	2.69
Friesian	42.39	0.04	1.86	0.53
Jersey	7.58	0.43	0.63	0.04
Montbéliarde	3.23	0.56	0.20	1.16

Table 3. Breed effect solutions (standard errors in parentheses) for the different reproductive traits relative to a Holstein.

	Friesian	Jersey	Montbéliarde
	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)
Age at first calving (days)	2.16 (3.18)	2.16 (3.18)	37.31 (4.48) ***
Age at first service (days)	2.91 (2.84)	4.30 (3.24)	20.95 (4.89) ***
Heifer calving rate (proportion)	-0.05 (0.02) **	0.02 (0.02)	-0.08 (0.03) ***
Heifer calving rate at 26 months (proportion)	-0.05 (0.02) *	0.02 (0.02)	-0.13 (0.03) ***
Heifer calving rate at 38 months (proportion)	-0.05 (0.02) **	0.01 (0.02)	-0.09 (0.03) ***
Calving rate in first 42 days calving season for primiparae (proportion)	0.04 (0.02) ***	0.03 (0.02)	-0.13 (0.03) ***
Calving to first service (days)	-0.83 (0.65)	-2.58 (0.78) ***	-3.56 (0.91) ***
Calving interval (days)	-5.02 (2.15) *	3.03 (2.50)	-3.40 (2.67)
Calving rate in first 42 days calving season for multiparae (proportion)	0.01 (0.03)	0.002 (0.01)	-0.03 (0.01)
Number of services	-0.05 (0.03)	0.04 (0.04)	-0.08 (0.04)
Pregnancy rate in first 42 days breeding season (proportion)	0.04 (0.02) *	0.04 (0.02)	0.03 (0.03)
Pregnancy rate to first service (proportion)	0.05 (0.03)	0.01 (0.03)	0.03 (0.03)
Submission rate in first 21 days breeding season (proportion)	0.03 (0.02)	0.07 (0.02) ***	0.01 (0.02)
Survival rate (proportion)	0.01 (0.01)	0.03 (0.01) ***	0.0003 (0.01)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ significance of difference from a Holstein.

Table 4. Breed-specific heterosis coefficients (standard errors in parentheses) for the different reproductive performance traits.

	Holstein × Friesian	Holstein × Jersey	Holstein × Montbéliarde	Friesian × Jersey	Friesian × Montbéliarde	Jersey × Montbéliarde
	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)
AFC	-5.84 (2.33) **	-6.90 (1.81) ***	-28.27 (3.09) ***	-3.58 (3.06)	-28.30 (4.88) ***	-22.95 (7.99) ***
AFS	-1.60 (1.54)	-2.38 (1.12) *	-10.04 (2.45) ***	-0.56 (1.89)	-16.24 (3.71) ***	-16.78 (5.35) ***
HCR	-0.02 (0.01)	0.01 (0.01)	0.03 (0.01)	0.01 (0.01)	0.02 (0.02)	0.05 (0.04)
HCR26	0.005 (0.01)	0.03 (0.01) ***	0.06 (0.02) ***	0.02 (0.02)	0.09 (0.03) ***	0.06 (0.04)
HCR38	-0.02 (0.01)	0.01 (0.01)	0.03 (0.01)	0.01 (0.01)	0.03 (0.02)	0.06 (0.04)
CR42_P	0.001 (0.02)	0.03 (0.01) **	0.04 (0.02)	-0.02 (0.02)	0.06 (0.04)	0.06 (0.06)
CFS	-0.90 (0.40) *	-1.40 (0.36) ***	-1.08 (0.51) *	0.11 (0.60)	-0.11 (0.94)	2.82 (1.70)
CIV	-6.68 (1.39) ***	-9.42 (1.24) ***	-9.56 (1.52) ***	-9.18 (2.11) ***	-7.92 (2.75) ***	-11.83 (5.70) *
CR42	0.02 (0.01) *	0.01 (0.01)	0.02 (0.01)	0.02 (0.01)	0.04 (0.02) *	0.08 (0.04) *
NS	-0.05 (0.02) **	-0.05 (0.02) **	-0.05 (0.03) *	-0.08 (0.03) **	-0.02 (0.05)	-0.02 (0.08)
PR42	0.07 (0.01) ***	0.06 (0.01) ***	0.06 (0.02) ***	0.07 (0.02) ***	0.06 (0.03) *	0.001 (0.05)
PRFS	0.03 (0.02)	0.05 (0.02) **	0.05 (0.02) *	0.05 (0.03)	0.04 (0.04)	0.09 (0.09)
SR21	0.02 (0.01)	0.04 (0.01) ***	0.05 (0.01) ***	0.01 (0.02)	-0.02 (0.02)	-0.04 (0.04)
SURV	0.02 (0.01) ***	0.03 (0.01) ***	0.04 (0.01) ***	0.03 (0.01) ***	0.04 (0.01) ***	0.03 (0.03)

AFC, age of first calving in days; AFS, age of first service in days; HCR, heifer calving rate (proportion); HCR26, heifer calving rate at 26 months of age (proportion); HCR38 heifer calving rate at 38 months of age (proportion); CR42_P, calving rate in first 42 days of calving season for primiparous cows (proportion); CFS, calving to first service in days; CIV, calving interval in days; CR42, calving rate in first 42 days of calving season for multiparous cows (proportion); NS, number of services; PR42, pregnancy rate in first 42 days of breeding season (proportion); PRFS, pregnancy to first service (proportion); SR21, submission rate in the first 21 days of breeding season (proportion); SURV, survival rate (proportion); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ significance of the coefficient from zero

Table 5. Breed-specific recombination loss coefficients (standard errors in parentheses) for the different reproductive performance traits.

	Holstein × Friesian	Holstein × Jersey	Holstein × Montbéliarde	Friesian × Jersey	Friesian × Montbéliarde	Jersey × Montbéliarde
	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)	<i>b</i> (s.e.)
AFC	-3.21 (3.76)	-8.41 (4.87)	10.52 (8.08)	-10.69 (10.32)	-34.43 (19.50)	74.42 (41.45)
AFS	-2.89 (2.89)	-0.71 (3.14)	7.39 (5.71)	-4.33 (6.64)	12.79 (13.32)	38.31 (23.73)
HCR	0.01 (0.02)	-0.001 (0.02)	0.03 (0.04)	-0.03 (0.05)	-0.11 (0.09)	0.05 (0.19)
HCR26	0.02 (0.02)	-0.001 (0.03)	0.05 (0.04)	-0.02 (0.05)	0.09 (0.10)	0.03 (0.22)
HCR38	0.02 (0.02)	-0.02 (0.02)	0.04 (0.04)	-0.03 (0.05)	-0.09 (0.09)	0.07 (0.19)
CR42_P	0.04 (0.03)	-0.03 (0.03)	0.05 (0.06)	0.10 (0.07)	0.25 (0.15)	0.10 (0.29)
CFS	-0.54 (0.76)	-1.21 (1.07)	0.48 (1.56)	0.82 (2.40)	-7.79 (4.49)	1.15 (9.32)
CIV	-3.21 (2.60)	-9.22 (3.82) *	-3.07 (5.20)	-15.37 (8.55)	8.30 (14.39)	3.30 (36.47)
CR42	-0.01 (0.01)	-0.01 (0.02)	0.07 (0.03) *	0.01 (0.05)	-0.01 (0.10)	-0.13 (0.21)
NS	-0.02 (0.04)	-0.06 (0.05)	0.03 (0.08)	-0.02 (0.12)	0.17 (0.22)	-0.61 (0.46)
PR42	0.03 (0.02)	0.03 (0.03)	0.03 (0.05)	0.003 (0.07)	0.10 (0.14)	0.21 (0.28)
PRFS	0.06 (0.03)	0.08 (0.06)	0.08 (0.07)	-0.06 (0.13)	-0.01 (0.20)	0.54 (0.44)
SR21	0.03 (0.02)	0.01 (0.03)	0.08 (0.04) *	-0.07 (0.06)	0.09 (0.12)	0.04 (0.24)
SURV	0.01 (0.01)	0.04 (0.01) **	0.01 (0.02)	-0.09 (0.04) **	0.02 (0.06)	-0.05 (0.15)

AFC, age of first calving in days; AFS, age of first service in days; HCR, heifer calving rate (proportion); HCR26, heifer calving rate at 26 months of age (proportion); HCR38 heifer calving rate at 38 months of age (proportion); CR42_P, calving rate in first 42 days of calving season for primiparous cows (proportion); CFS, calving to first service in days; CIV, calving interval in days; CR42, calving rate in first 42 days of calving season for multiparous cows (proportion); NS, number of services; PR42, pregnancy rate in first 42 days of breeding season (proportion); PRFS, pregnancy to first service (proportion); SR21, submission rate in the first 21 days of breeding season (proportion); SURV, survival rate (proportion); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ significance of the coefficient from zero.

Variance components

Heritability estimates for the reproductive traits in heifers and cows ranged from 0.004 (PRFS) to 0.04 (HCR); the exception was AFS, which had a heritability of 0.17 (Table 1). Repeatability estimates of the reproductive traits varied from 0.01 (CIV and PRFS) to 0.11 (PR42). The permanent environment component accounted for 0.01 (CR42) to 0.09 (PR42) of the phenotypic variation in the reproductive traits. The coefficient of genetic variation for the continuous reproductive performance traits ranged from 0.01 (AFC) to 0.05 (NS) while the coefficient of permanent environmental variation varied from 0.002 (CIV) to 0.11 (NS). The genetic standard deviation of the nine binary traits varied from 0.02 (CR42) to 0.07 (HCR) and the permanent environment standard deviation of the nine binary traits varied from 0.001 (SURV) to 0.13 (PR42).

Correlations

Genetic and phenotypic correlations among the reproductive traits are given in Table 6. Permanent environmental and residual correlations among the reproductive traits are presented in Table 7. The phenotypic and residual correlations were both generally weaker than the corresponding genetic and permanent environmental correlations.

In general, the heifer calving rate traits (HCR, HCR26 and HCR38) were more strongly genetically correlated to other nulliparous reproductive performance traits than to multiparous reproductive performance traits. Increased HCR26 was strongly genetically associated with a younger age at first service ($r = -0.76$) and age at first calving ($r = -0.97$). Although the genetic correlations between HCR26 and some multiparous reproductive traits were approximately null (between -0.07 and 0.13 for CFS, PRFS, PR42 and CR42), an increased HCR26 was weakly to moderately genetically associated with greater SR21 ($r = 0.21$), fewer NS ($r = -0.22$), increased SURV ($r = 0.28$) and shorter CIV ($r = -0.34$). Longer CFS was genetically associated with both a reduced submission rate ($r = -0.98$) and reduced pregnancy rate in the first 42 days of the breeding season ($r = -0.69$). CFS explained 56% of the genetic variation in CIV. A genetically shorter CIV was associated with superior genetic merit for establishing pregnancy to first service, as well as pregnancy establishment in the first 42 days of the breeding season. Genetically shorter CIV was also moderately correlated with improved submission rate ($r = -0.70$) and fewer services ($r = 0.63$). Phenotypic correlations between CR42 for primiparous cows and all other reproductive performance traits were close to zero.

Table 6. Genetic (above the diagonal; standard error in parenthesis) and phenotypic (below the diagonal; standard error in parenthesis) correlations between the reproductive performance traits.

	AFC	AFS	HCR	HCR26	HCR38	CR42_P	CFS	CIV	CR42	NS	PR42	PRFS	SR21	SURV
AFC		0.62 (0.004)	-0.01 (0.006)	-0.81 (0.002)	-0.21 (0.005)	-0.98 (0.130)	0.07 (0.201)	-0.13 (0.231)	-0.81 (0.179)	0.14 (0.215)	-0.26 (0.191)	-0.22 (0.212)	-0.30 (0.180)	-0.52 (0.134)
AFS	0.99 (0.003)		-0.08 (0.005)	-0.36 (0.006)	-0.08 (0.007)	0.28 (0.223)	0.47 (0.083)	-0.19 (0.117)	-0.80 (0.092)	-0.24 (0.115)	0.05 (0.111)	0.06 (0.126)	0.09 (0.100)	-0.04 (0.086)
HCR	-0.66 (0.128)	0.04 (0.088)		0.99 (0.007)	0.99 (0.0004)	0.56 (0.229)	-0.07 (0.120)	-0.28 (0.132)	-0.65 (0.149)	-0.22 (0.133)	-0.08 (0.124)	-0.10 (0.139)	0.12 (0.112)	0.08 (0.104)
HCR26	-0.97 (0.016)	-0.76 (0.044)	0.78 (0.002)		0.99 (0.006)	0.77 (0.194)	-0.07 (0.127)	-0.34 (0.133)	0.13 (0.226)	-0.22 (0.138)	0.09 (0.130)	0.08 (0.145)	0.21 (0.116)	0.28 (0.105)
HCR38	-0.84 (0.067)	0.01 (0.091)	0.99 (0.0001)	0.78 (0.002)		0.58 (0.233)	-0.03 (0.123)	-0.29 (0.134)	-0.66 (0.150)	-0.24 (0.134)	-0.09 (0.126)	-0.07 (0.142)	0.09 (0.114)	0.10 (0.106)
CR42_P	-0.29 (0.010)	0.004 (0.004)	-0.09 (0.014)	0.14 (0.013)	-0.06 (0.014)		0.19 (0.228)	-0.12 (0.299)	0.07 (0.027)	0.05 (0.279)	0.15 (0.258)	0.45 (0.278)	0.32 (0.231)	0.19 (0.251)
CFS	-0.06 (0.011)	0.02 (0.003)	0.004 (0.015)	0.04 (0.013)	0.02 (0.015)	0.21 (0.006)		0.75 (0.074)	-0.40 (0.214)	-0.10 (0.134)	-0.69 (0.082)	-0.26 (0.139)	-0.98 (0.023)	-0.37 (0.092)
CIV	-0.02 (0.008)	-0.004 (0.003)	0.02 (0.010)	0.002 (0.009)	0.02 (0.010)	0.06 (0.007)	0.24 (0.004)		-0.57 (0.192)	0.63 (0.098)	-0.96 (0.029)	-0.90 (0.060)	-0.70 (0.081)	-0.72 (0.074)
CR42	0.18 (0.287)	-0.02 (0.003)	0.25 (0.265)	-0.10 (0.265)	0.09 (0.201)	0.008 (0.003)	0.24 (0.004)	0.05 (0.003)		-0.009 (0.004)	0.06 (0.004)	0.05 (0.003)	0.10 (0.004)	0.35 (0.174)
NS	0.01 (0.012)	-0.005 (0.003)	0.03 (0.016)	0.02 (0.014)	0.02 (0.016)	-0.02 (0.006)	-0.13 (0.003)	0.51 (0.003)	-0.43 (0.172)		-0.66 (0.085)	-0.94 (0.032)	0.09 (0.003)	-0.72 (0.077)
PR42	-0.02 (0.013)	0.002 (0.003)	0.02 (0.018)	0.07 (0.016)	0.03 (0.018)	0.02 (0.006)	-0.16 (0.003)	-0.65 (0.002)	0.89 (0.086)	-0.54 (0.002)		0.63 (0.002)	0.24 (0.003)	0.84 (0.047)
PRFS	-0.005 (0.0005)	0.001 (0.003)	-0.0008 (0.001)	0.0005 (0.0009)	-0.0006 (0.001)	0.003 (0.0006)	0.02 (0.003)	-0.48 (0.004)	0.87 (0.134)	-0.71 (0.008)	0.97 (0.026)		0.07 (0.003)	0.79 (0.069)
SR21	-0.03 (0.012)	0.003 (0.003)	0.02 (0.016)	0.08 (0.015)	0.02 (0.016)	0.04 (0.006)	-0.48 (0.002)	-0.15 (0.004)	0.95 (0.110)	-0.13 (0.125)	0.81 (0.055)	0.55 (0.105)		0.35 (0.091)
SURV	-0.02 (0.008)	-0.001 (0.003)	-0.10 (0.010)	0.004 (0.009)	-0.04 (0.010)	-0.04 (0.007)	-0.05 (0.004)	-0.06 (0.004)	0.01 (0.004)	-0.10 (0.003)	0.22 (0.0006)	0.12 (0.001)	0.05 (0.004)	

AFC, age of first calving; AFS, age of first service; HCR, heifer calving rate; HCR26, heifer calving rate at 26 months of age; HCR38 heifer calving rate at 38 months of age; CR42_P, calving rate in first 42 days of calving season for primiparous cows; CFS, calving to first service; CIV, calving interval; CR42, calving rate in first 42 days of calving season for multiparous cows; NS, number of services; PR42, pregnancy rate in first 42 days of breeding season; PRFS, pregnancy to first service; SR21, submission rate in the first 21 days of breeding season; SURV, survival rate.

Cows with permanent environmental effects for a shorter CIV had, on average also permanent environment effects for a greater SR21, PR42, PRFS and CR42. The permanent environmental effects for a shorter CFS were also strongly associated with the permanent environmental effects for longer CIV ($r=-0.99$), more services ($r=-0.93$) and superior pregnancy rate in the first 42 days of the breeding season ($r=0.83$). A greater PR42 was also associated with a greater SR21 ($r=0.80$) and fewer services ($r=-0.65$), at the permanent environmental level.

Prediction of future cow reproductive performance

The ability of the three alternative approaches to predict future cow reproductive performance is shown in Table 8. Irrespective of reproductive performance trait, the reproductive

performance index (composed of additive genetic effects, non-additive genetic effects and permanent environmental effects) and the adjusted phenotype were better predictors of subsequent reproductive performance than predictions based solely on EBV. The reproductive performance index accounted for 0.5% (CFS and PRFS) to 4% (SURV) of the variation in the phenotypes of the individual in 2011, whereas the EBVs explained between 0.1% (CFS) to 0.8% (PR42) of the variation for the phenotypic value in the validation population.

Discussion

The objective of this study was to estimate not only the additive genetic variance components for a range of reproductive traits

Table 7. Permanent environmental (above the diagonal; standard error in parenthesis) and residual (below the diagonal; standard error in parenthesis) correlations between the reproductive performance traits.

	AFC	AFS	HCR	HCR26	HCR38	CR42_P	CFS	CIV	CR42	NS	PR42	PRFS	SR21
AFS	0.59 (0.004)												
HCR	-0.009 (0.006)	-0.09 (0.004)											
HCR26	-0.81 (0.002)	-0.35 (0.005)	0.78 (0.001)										
HCR38	-0.20 (0.005)	-0.09 (0.006)	0.99 (0.0001)	0.78 (0.002)									
CR42_P	-0.29 (0.010)	0.006 (0.004)	-0.09 (0.015)	0.14 (0.013)	-0.07 (0.015)								
CFS	-0.06 (0.011)	0.0 [§]	0.005 (0.015)	0.04 (0.014)	0.02 (0.015)	0.21 (0.006)		-0.99 (0.273)	-0.04 (0.062)	-0.93 (0.052)	0.83 (0.07)	0.95 (0.092)	-0.60 (0.035)
CIV	-0.02 (0.008)	0.0 [§]	0.02 (0.010)	0.005 (0.009)	0.02 (0.010)	0.06 (0.007)	0.27 (0.004)		-0.95 (0.111)	0.40 (0.090)	-0.96 (0.048)	-0.79 (0.086)	-0.99 (0.096)
CR42	0.19 (0.297)	0.62 (0.042)	0.26 (0.277)	-0.11 (0.275)	0.10 (0.209)	0.0 [§]	0.26 (0.005)	0.0 [§]		0.0 [§]	-0.02 (0.005)	0.0 [§]	0.03 (0.050)
NS	0.01 (0.012)	0.0 [§]	0.04 (0.017)	0.02 (0.015)	0.03 (0.016)	-0.02 (0.006)	-0.08 (0.004)	0.52 (0.003)	0.0 [†]		-0.65 (0.026)	-0.87 (0.023)	0.11 (0.004)
PR42	-0.02 (0.014)	0.0 [§]	0.02 (0.019)	0.07 (0.017)	0.03 (0.019)	0.02 (0.007)	-0.22 (0.004)	-0.64 (0.003)	0.94 (0.058)	-0.53 (0.003)		0.60 (0.001)	0.18 (0.004)
PRFS	0.0 [§]	0.0 [§]	0.0 [§]	0.0 [§]	0.0 [§]	0.0 [§]	0.0 [§]	-0.48 (0.002)	0.99 (0.044)	-0.72 (0.001)	0.93 (0.019)		0.03 (0.004)
SR21	-0.03 (0.013)	0.0 [§]	0.02 (0.017)	0.09 (0.015)	0.02 (0.017)	0.04 (0.006)	-0.47 (0.003)	-0.10 (0.005)	0.86 (0.045)	-0.12 (0.043)	0.80 (0.027)	0.54 (0.049)	
SURV	-0.02 (0.008)	0.0 [§]	-0.10 (0.010)	0.004 (0.009)	-0.04 (0.010)	-0.05 (0.007)	-0.05 (0.004)	-0.06 (0.004)	0.01 (0.004)	-0.10 (0.004)	0.0 [§]	0.0 [§]	0.06 (0.004)

AFC, age of first calving; AFS, age of first service; HCR, heifer calving rate; HCR26, heifer calving rate at 26 months of age; HCR38 heifer calving rate at 38 months of age; CR42_P, calving rate in first 42 days of calving season for primiparous cows; CFS, calving to first service; CIV, calving interval; CR42, calving rate in first 42 days of calving season for multiparous cows; NS, number of services; PR42, pregnancy rate in first 42 days of breeding season; PRFS, pregnancy to first service; SR21, submission rate in the first 21 days of breeding season; SURV, survival rate [§]Residual correlations set to zero; [†] Non-estimable

Table 8. Correlations between the phenotype in the validation population with the respective adjusted phenotype, estimated breeding value, and reproductive performance index for multiparous reproductive performance traits estimated in the calibration dataset.

Validated phenotype	Adjusted phenotype	Estimated breeding value	Reproductive performance index
Calving to first service (days)	0.07	0.03	0.07
Calving interval (days)	0.09	0.08	0.10
Submission rate in first 21 days breeding season	0.09	0.06	0.09
Number of services	0.08	0.07	0.08
Pregnancy rate to first service	0.08	0.06	0.07
Pregnancy rate in first 42 days breeding season	0.14	0.09	0.13
Survival rate	0.14	0.08	0.20

but also the contribution of additional sources of variability (non-additive genetic and permanent environmental effects) to phenotypic differences in reproductive performance in nulliparous, primiparous and multiparous seasonal-calving dairy cows. Such alternative sources of variation could provide a more accurate prediction of future cow performance compared with that predicted by additive genetic merit alone, and provide

credence to the development of an index to rank dairy females more aligned to their phenotypic reproductive performance. Data used in genetic evaluations for reproductive performance internationally are almost exclusively from cows. Heifers that die or are culled without producing a calf are therefore not considered in the evaluations. Such an omission may bias the genetic evaluations for reproductive performance by over-

estimating the reproductive potential of genetically inferior heifers for reproductive performance. A total of 23% of heifers in the present study failed to ever calve in their lifetime, corroborating the statistic of 26% documented by Wathes *et al.*, (2008) in UK dairy heifers. Substantial economic losses ensue because of the total cost of a replacement heifer, which has been estimated to be €1545 (Shalloo *et al.*, 2014). Therefore, minimising the number of replacements to rear, as well as only identifying the most reproductively efficient heifers, is essential to avoid unnecessary economic losses. The current study presented novel traits for nulliparae reproductive performance that could negate such reproductive inefficiencies and associated financial costs. The trend observed in the heifer calving rate traits (i.e. almost a quarter of heifers failing to enter the milking herd) justified the investigation of the genetic and environmental components attributable to the phenotypic performance of nulliparae reproduction.

Excellent reproductive performance in seasonal dairy systems require calving intervals that are within a calendar year and are achieved through a quick return to service post-calving and high pregnancy rates (Berry *et al.*, 2013). Seasonal dairy production systems rely on excellent reproductive performance to align the period of calving with the initiation of rapid grass growth to maximise the utilisation of low-cost grazed grass in the diet (Crosse *et al.*, 1994). Controlled experiments in Irish research herds have shown that optimum reproductive targets for seasonal calving production systems are currently not being achieved (Coleman *et al.*, 2009; Cummins *et al.*, 2012) and results from Irish national data (Evans *et al.*, 2006; Berry *et al.*, 2013) further substantiate this sub-optimum reproductive performance. Results from the large sample population used in the current study, which included a proportion of crossbred cows (at least 10% of cows per herd were crossbred), revealed an improved performance in reproduction efficiency, albeit some reproductive performance targets were still below optimum. While the current study dataset used similar reproductive performance traits and spring-calving cows as in Berry *et al.*, (2013), the improvement in reproductive performance may be attributable to the selection of spring-calving crossbred herds because of the associated favourable heterosis effects on reproductive performance (Table 4).

Additive genetic effects

Although the heritability estimates for most of the reproductive performance traits in the present study were low, corroborating studies in dairy seasonal calving (Olori *et al.*, 2002; Berry *et al.*, 2004; Berry *et al.*, 2013) and confinement production systems (Lucy, 2001; Wall *et al.*, 2003; Liu *et al.*, 2008), genetic variation in reproductive performance was nonetheless detected. The coefficient of genetic variation

for the continuous reproductive traits (ranged from 0.01 to 0.05) was consistent with the documented estimates in other populations (Grosshans *et al.*, 1997; Olori *et al.*, 2002), but was also similar to reported coefficients of genetic variation for other performance traits like live-weight, body condition score and milk yield (Berry *et al.*, 2003; Mc Hugh *et al.*, 2012). This therefore signifies potential to improve reproductive performance through a well-structured breeding programme that can achieve high accuracy of selection for lowly heritable reproductive traits. Nonetheless, the observed low heritability of the multiparous reproductive traits in the present study was reflected in poor predictive ability of individual cow future reproductive performance from EBV (Table 8).

Of particular relevance in the present study were the heritability estimates of 0.04 for all heifer calving rate traits (HCR, HCR26 and HCR38). These were the highest heritability estimates of all the reproductive performance traits evaluated in the present study, with the exception of age at first service (0.17). Whether or not a heifer calves within her lifetime is a vital element in maintaining optimum economic performance of the herd by minimising the non-productive period of the animal's life (Wathes *et al.*, 2014). Therefore, genetic selection provides an opportunity to improve heifer calving rate from the current rate of only 77% of heifers ever calving within their lifetime, as well as increasing the proportion of heifers calving within 26 months of birth. The presence of genetic variation for heifer calving rate traits support the argument for publishing the breeding values of heifer calving rate traits to identify sires that have more daughters entering the herd. Genetic correlations between the heifer calving rate traits and other nulliparae reproductive traits were generally strong and favourable, owing to the part-whole relationship between nulliparae traits; therefore, selection for improved nulliparae reproductive performance in one trait will indirectly select for improved nulliparae performance in another. Moreover, the lack of genetic correlations between nulliparous and multiparous traits suggests that current breeding programmes that include multiparous reproductive performance are not indirectly improving reproductive performance in nulliparous heifers.

Calving interval, or similar traits like days open or calculated daughter pregnancy rate (VanRaden *et al.*, 2004), are commonly used measures of reproductive performance in dairy cow breeding goals. Such traits may not be optimal for seasonal calving (and therefore breeding) herds. This is because breeding in seasonal production herds begins on a defined calendar date; therefore, a cow calving very early in the calving season is, on average, likely to have a longer CIV than a cow calving later in the calving season. Therefore, a fertile early calving cow could have the same CIV as a sub-fertile cow calving later in the calving season whereby the CIV for the latter cow was due to inferior reproductive performance (e.g.

anoestrus). Although adjustment for contemporary group in the statistical model may partly account for such a phenomenon, it may not be optimal as animals calving within several weeks of each other may constitute the same contemporary group. Moreover, CIV (and similar traits) requires information on date of conception or a subsequent calving date. This delays achieving high accuracy of selection for reproductive performance in young animals and is particularly relevant in the era of genomic selection (Meuwissen *et al.*, 2001) in seasonal breeding herds when bulls enter widespread use at a younger age (Spelman *et al.*, 2013). Furthermore, the least fertile animals (i.e. those that are infertile) do not have a phenotypic value for CIV. Reproductive performance measures, other than CIV, could be used as an alternative to address the shortcomings of CIV. Embedded within CIV are CFS, PRFS and NS. Use of such genetically correlated reproductive performance component traits (Table 6) would facilitate a reduction in the time interval required to obtain a prediction of genetic merit for CIV where a subsequent calving date does not yet exist, thus providing an earlier measure of reproductive performance. For example, calving to first service explained 56% of the genetic variance in CIV.

Of particular relevance in seasonal calving grazing herds to maximising the exploitation of low-cost grazed grass in the diet is the proportion of cows calving early after the planned start of the calving season. Using the genetic standard deviation for CR42 of 0.02, the difference in the mean proportion of cows in the top versus bottom 20 percentile in genetic merit for CR42 is expected to be 7 percentage units. The current study reported that 70% of cows calve within the first 42 days of the calving season and therefore the genetic variation present for the CR42 trait suggests that there is an opportunity to improve this statistic even further through genetic selection.

Breed and non-additive genetic effects

The favourable reproductive performance in the JE compared to the HO has been documented by others corroborating the results from the present study. For instance, relative to the HO, higher pregnancy rates (VanRaden and Sanders, 2003), higher conception rates and fewer services per conception (Badinga *et al.*, 1985), as well as shorter CFS (Grosshans *et al.*, 1997; Prendiville *et al.*, 2011), have been observed in the JE. Similar to findings by Walsh *et al.*, (2008), HO generally outperformed the MO in the majority of reproductive performance traits in the present study. This is in direct contrast to a French study that reported a 13-day shorter calving to first service interval in the MO compared to the HO (Barbat *et al.*, 2010). Differences between the studies may be attributable to the different systems of production and different mean reproductive performance; the genetic background of both breeds may also have differed between the studies. For

instance, the average CIV for HO in France was 408 days in 2006; median CIV for the period between the years 2006 and 2012 in the present study was 369 days (Table 3).

The merits of cross-breeding have been discussed in detail elsewhere (VanRaden and Sanders, 2003; Freyer *et al.*, 2008; Kargo *et al.*, 2012; Buckley *et al.*, 2014). Cross-breeding strategies aim to exploit the enhanced performance associated with heterosis, as well as capitalise on the introgression of favourable alleles from different breeds with good complementarity. Rapid gains in performance can be achieved due to the reduction of the unfavourable consequences of inbreeding depression, especially for lowly heritable traits, such as reproductive performance and longevity. The superior reproductive performance in F_1 crossbreds, compared to the parental purebred for the majority of reproductive performance traits in the present study was therefore not unexpected. The heterosis effects were favourable for all traits, ranging from 0.1% to 18% of the mean for CR42 in primiparae (mean of 84%) and PRFS (mean of 52%), respectively. Similar conclusions have emerged from controlled experiments (Heins *et al.*, 2008; Begley *et al.*, 2009; Prendiville *et al.*, 2011) and the analysis of national data (McAllister *et al.*, 1994; Wall *et al.*, 2005; Penasa *et al.*, 2010; Coffey *et al.*, 2014). Buckley *et al.*, (2014) documented that heterosis in Holstein–Friesian Jersey crossbreds increases the probability of a cow having a calf born to artificial insemination during the calving period by 3.4%. This finding corroborates the present study findings of 2.8%, 1.6% and 2.6% of the mean of a similar trait, calving rate in the first 42 days of the breeding season, for HO×FR, HO×JE, and FR×JE crossbreds, respectively. In general, the heterosis effects were greater in crosses of more diverse breeds (Lopez-Villalobos and Garrick 2002). In general, breed-specific recombination losses were not associated with the reproductive performance in the current study, therefore implying that the epistatic loss of linked loci did not cause deterioration in reproductive performance. The quantification of extra gain in performance due to heterosis is currently not included in the national breeding goal or mating advice tools. In Ireland, research undertaken by the ICBF indicated that the economic heterosis effects contributed €100 per lactation in the F_1 cross, owing primarily to improved milk revenues and large differences in reproductive efficiency and longevity observed with the cross-bred herds (Buckley *et al.*, 2014). The relative importance of including non-additive genetic differences is considerably greater for cross-breds from divergent parental breeds, especially for lowly heritable traits such as reproductive performance. This means that ranking cow performance based on EBV alone would be expected to underestimate the future profit potential of the cross-bred cow's actual future performance as additive genetic merit ignores the extra gain in performance due to cross-breeding.

Permanent environment effects

Permanent environmental effects are environmental effects that contribute permanently to an individual's phenotype, are constant across repeated measures (Kruuk and Hadfield, 2007) and are cumulative over time (Schaeffer, 2011). In addition, there is emerging evidence of the long-term impact of environmental perturbations on offspring phenotype (Gicquel *et al.*, 2008; Singh *et al.*, 2010). Epigenetic effects are changes in gene expression caused by DNA and histone modifications, which are responsible for modulation of regulatory genes, without changing the DNA sequence (Wolffe and Guschin, 2000; Bird, 2002). For example, intrauterine environment stimuli may impact foetal development and this permanently affects phenotypic performance later in life (Berry *et al.*, 2008); such epigenetic modifications may be broken down into foetal reprogramming of subsequent progeny, thus resulting in permanent environmental effects that are not transmitted across generations and thus do not enter the genetic variation component.

In the present study, permanent environmental effects had a similar or even greater contribution to the phenotypic variation in reproductive performance ($c^2=0.01$ to 0.09) than the additive genetic effects ($h^2=0.004$ to 0.04 ; Table 1). This highlights the importance of the permanent environmental influence on the phenotypic expression of these lowly heritable traits. Inclusion of such permanent environment effects into an index of reproductive performance should rank dairy females more accurately to their phenotypic performance. This was substantiated by the index analysis in the current study; a stronger association was observed between the cow reproductive performance index, which included permanent environmental effects with future phenotypic reproductive performance of cows, compared to the correlations between EBV and future reproductive performance.

The permanent environmental correlations among the reproductive performance traits were generally stronger than those reported by Haile-Mariam *et al.*, (2003) between similar traits. Irrespective of whether permanent environmental effects

are an artefact of epigenetic effects or based only on previous management influences, cows with a deleterious permanent environment effect for a reproductive performance trait will generally have unfavourable reproductive performance in the other aspects of reproductive performance. For example, the permanent environmental component of CIV is a manifestation of the permanent environmental components of its contributing traits such as calving to first service interval, submission rate and conception rate, as evidenced by the strong permanent environmental correlations with CIV.

Conclusions

Maintaining a herd with optimal reproductive performance is paramount in a seasonal-calving dairy production system. Better reproductive performance can be achieved through the appropriate breeding programme that exploits genetic variation in reproductive performance. Although the heritability of the reproductive traits in the present study was low, genetic variation existed, suggesting that once a well-structured breeding programme was in place, high accuracy of selection could be achieved and genetic gain in reproductive performance realised. Results from this study indicate that inclusion of non-additive genetic and permanent environment effects, as well as additive effects, into an index would provide more accurate predictions of dairy female reproductive performance. An extension of the cow reproductive performance index developed here might be justified to provide a decision support tool for producers based on traits of economic importance, including reproductive performance.

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