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Milk production and fertility performance of Holstein, Friesian, and Jersey purebred cows and their respective crosses in seasonal-calving commercial farms

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ABSTRACT

There is renewed interest in dairy cow crossbreeding in Ireland as a means to further augment productivity and profitability. The objective of the present study was to compare milk production and fertility performance for Holstein, Friesian, and Jersey purebred cows, and their respective crosses in 40 Irish spring-calving commercial dairy herds from the years 2008 to 2012. Data on 24,279 lactations from 11,808 cows were available. The relationship between breed proportion, as well as heterosis and recombination coefficients with performance, was quantified within a mixed model framework that also contained the fixed effects of parity; cow and contemporary group of herd-year-season of calving were both included as random effects in the mixed model. Breed proportion was associated with all milk production parameters investigated. Milk yield was greatest for Holstein (5,217 kg), intermediate for Friesian (4,591 kg), and least for Jersey (4,230 kg), whereas milk constituents (i.e., fat and protein concentration) were greatest for Jersey (9.38%), intermediate for Friesian (7.91%), and least for Holstein (7.75%). Yield of milk solids in crossbred cows exceeded their respective parental average performance; greatest milk solids yield (i.e., fat kg + protein kg) was observed in the Holstein × Jersey first-cross, yielding 25 kg more than the mid-parent mean. There was no consistent breed effect on the reproductive traits investigated. Relative to the mid-parent mean, Holstein × Jersey cows calved younger as heifers and had a shorter calving interval. Friesian × Jersey first-cross cows also had a shorter calving interval relative to their mid-parent mean. Results were consistent with findings from smaller-scale controlled experiments. Breed complementarity and heterosis attainable from crossbreeding resulted in superior animal performance and, consequently, greater expected profitability in crossbred cows compared with their respective purebreds.
Key words: crossbreeding, Jersey, heterosis, Holstein, Friesian

INTRODUCTION

The process of producing more food while reducing environmental impact has become a global challenge and requires what has been referred to as "sustainable intensification" (Pretty, 1997) of global agricultural production. In this context, there is an increasing appreciation of the multifunctional characteristics and benefits of grassland farming (Jeangros and Thomet, 2004; Baumont et al., 2014; Taube et al., 2014) and previous studies have highlighted the potential for highly productive and environmentally benign grass-based milk production (Lyons et al., 2008; Peyraud et al., 2010; McCarthy et al., 2015). Although a diverse range of grazing systems are practiced internationally, many of which are economically competitive across a wide range of countries and climatic conditions (Soder and Rotz, 2001; Dillon et al., 2005; Roche et al., 2009), such systems represent only a small minority of global milk production (~10%; Steinfeld and Maki-Hokkonen, 1995). Furthermore, the biological and financial efficiency of milk production in predominantly grazing systems, such as those practiced in Ireland (where grazed pasture is the primary source of nutrients), is uniquely dependent on an integrated seasonal production model. A wide variety of factors such as stocking rate (McCarthy et al., 2013), concentrate supplementation rate (Kennedy et al., 2003), and animal genetic merit (McCarthy et al., 2007; Macdonald et al., 2008) affect grazing system performance.

The selection of appropriate animals for grazing systems is uniquely complicated by the elevated importance of reproductive performance in such systems to calve compactly at the beginning of the grass-growing

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season thereby having abundant high-quality pasture in early lactation and during rebreeding (O'Mara, 2008; Washburn and Mullen, 2014). To achieve this objective, the national economic breeding index (**EBI**) was developed in 2001 and reflects the profit per lactation of progeny within Irish dairy systems (Berry et al., 2014; Ramsbottom et al., 2015). The EBI currently includes 18 traits and the relative emphases on milk production and reproductive performance traits are 33 and 35%, respectively (Berry et al., 2014). In both controlled (Coleman et al., 2010) and commercial (Ramsbottom et al., 2012) evaluations, greater EBI has been associated with increased farm profitability compared with animals of lower EBI by virtue of increased productivity and improved reproductive performance. Previous studies both in experimental herds in Ireland (Buckley et al., 2007; Prendiville et al., 2009; Vance et al., 2012) and within larger population studies internationally (Falconer et al., 1996; Lopez-Villalobos et al., 2000a; Lopez-Villalobos and Garrick, 2002; Grainger and Goddard, 2004; Buckley et al., 2014) have demonstrated additional benefits of crossbreeding on animal performance and financial efficiency by exploiting both additive and nonadditive genetic effects (Ahlborn-Breier and Hohenboken, 1991). However, the extent of dairy crossbreeding on commercial farms in Ireland remains low, with crossbred cows accounting for just 5.2% of the Irish national dairy herd (Department of Agriculture, 2014).

The objective of the present study was to compare the biological performance of Holstein, Friesian, and Jersey purebred cows and Holstein × Jersey and Friesian × Jersey crossbred cows using a large data set of 40 commercial dairy herds practicing crossbreeding in Ireland over a 5-yr period. Results from this large study will be useful for dairy producers to evaluate the potential of crossbreeding strategies to maximize production efficiency and profitability within grass-based systems in the future.

MATERIALS AND METHODS

Information from the Irish Cattle Breeding Federation database on 11,808 cows from 40 spring-calving dairy herds that adopted crossbreeding between Holstein, Friesian and Jersey breeds for each of the years 2008 to 2012 inclusive were available. A spring-calving dairy herd was defined as a herd in which >80% of cows calved between January 1 and May 31 in each year of the study and represents the predominant herd type in Ireland (Berry et al., 2013). Thirty-nine of the herds contained some purebred Holstein-Friesian cows, and 5 of the herds contained some purebred Jersey cows; all herds contained Holstein-Friesian × Jersey crossbred cows. The number of cows, number of lactations, and average parity of each breed and cross are in Table 1. The cows included in the study were of high total genetic merit, with an average EBI of €159. Available data included milk production lactation performance [i.e., milk yield (kg), fat yield (kg), protein yield (kg), and SCC], date of birth, calving date, parity, service dates, and pregnancy diagnosis.

Table 1. Number of cows and lactation records and average parity for the different breeds and crosses used in the present study

Breed[1]	Cows	Lactations	Parity
HO	1,091	2,413	3.07
FR	16	53	2.91
JE	409	1,022	3.58
HO×FR	108	247	3.74
HO×JE	883	2,241	3.30
FR×JE	18	50	2.94
HO × HO×FR	3,951	8,716	3.08
FR × HO×FR	303	762	3.44
HO × HO×JE	3,757	8,427	2.96
JE × HO×JE	1,967	4,871	3.31
FR × FR×JE	52	138	2.89
JE × FR×JE	861	2,145	3.53
HO×FR × HO×FR	3,941	8,929	3.09
HO×JE × HO×JE	3,394	7,707	2.95
FR×JE × FR×JE	471	1,169	3.46

[1]HO = Holstein, FR = Friesian, JE = Jersey, HO×FR = Holstein-Friesian first-cross, HO×JE = Holstein-Jersey first-cross, FR×JE = Friesian-Jersey first-cross, HO × HO×FR = HO sire × HO×FR dam, FR × HO×FR = FR sire × HO×FR dam, HO × HO×JE = HO sire × HO×JE dam, JE × HO×JE = JE sire × HO×JE dam, FR × FR×JE = FR sire × FR×JE dam, JE × FR×JE = JE sire × FR×JE dam; a purebred animal was deemed to be ≥87.5% of the breed.

Milk Production

Data consisted of 305-d milk production yield (i.e., milk kg, fat kg, protein kg, and SCC) on 24,279 lactations from 10,593 cows. Obvious data errors were removed. Milk volume yields <2,000 or >12,000 kg were discarded. Milk fat yields or milk protein yields <100 and >500 kg were also discarded. Somatic cell count <1,000 or >999,000 cells/mL were discarded; SCC was transformed to SCS using the logarithm to the base 10.

Fertility

Calving dates of 24,706 lactations from 10,625 cows were available. A total of 70,645 service dates were also available. Age at first calving was defined as the age at which heifers first calved; only age at first calving records between 550 and 1,250 d were retained. Calving to first service interval was defined for all cows as the number of days from calving to first service; only calving to first service records between 10 and 250 d were retained. The start of a herd's calving season for multiparous cows was defined as the first date of a 14-d period within which at least 5 multiparous cows calved. Calving in the first 42 d of the calving season was defined as whether or not a cow calved in the first 42 d of the calving season. Cows that calved in the 14 d before the start of the calving season were deemed to have calved in the first 42 d of the calving season, to account for short gestation and premature births; 3 cows calved in the 14-d period before the start of the defined calving season. Calving interval was defined as the number of days between consecutive calvings; only calving interval records between 300 and 800 d were retained.

The start of the herd's breeding season was defined as the first date of a 14-d period within which at least 5 cows were served. The end of the herd breeding season was defined as the last service where no subsequent service was recorded within 21 d. Only breeding seasons between 35 and 140 d in length with at least 20 cows were retained. Submission rate was defined as whether or not a cow was served in the first 21 d of the breeding season, regardless of calving date. Calving to first service and submission rate records were discarded for herd-years where >80% of cows were recorded to have received just one insemination; this was undertaken to remove herd-years that only recorded the last insemination, and 3 such herd-years were discarded.

Pairwise breeding-specific heterosis and recombination coefficients for each animal were calculated as

$$1-\sum_{i=1}^{2} sire_i \cdot dam_i$$

and

$$1-\sum_{i=1}^{2} \frac{sire_i^2 + dam_i^2}{2},$$

respectively, where $sire_i$ and dam_i are the proportion of breed i in the sire and dam, respectively (VanRaden and Sanders, 2003).

Statistical Analyses

Contemporary groups of herd-year-season of calving were generated based on the algorithm described in detail by Berry et al. (2013). The algorithm grouped animals together, within herd, based on calving dates of close proximity. Contemporary group was defined separately for each trait. Only contemporary groups with 5 or more animals were retained. The numbers of records retained for analysis are in Table 2 and Table 3 for milk production and reproduction traits, respectively. Parity was defined after calving and parity structure varied per trait but was approximately 26, 21, 17, 12, and 24% for parities 1, 2, 3, 4, and ≥5, respectively.

Linear mixed models and generalized estimating equations in ASREML (Gilmour et al., 2011) were used to estimate the relationship between both breed and nonadditive genetic coefficients on a series of traits. Linear mixed models were used to estimate least squares means for milk production and interval reproduction traits. Generalized estimating equations with a logit link function were used to estimate predicted probabilities for the binary traits assuming a binomial distribution of the error. Fixed effects in the model included the proportion of each breed; that is, Holstein (**HO**), Friesian (**FR**), and Jersey (**JE**), breed-specific heterosis (i.e., HO×FR, HO×JE, and FR×JE) and breed-specific recombination (i.e., HO×FR, HO×JE, and FR×JE) all fitted as continuous effects; parity (1, 2, 3, 4, ≥5) was included as a class effect. Both cow and contemporary group were included as random effects.

Table 2. Number of records, mean and standard deviation estimates for milk production traits in the population

Trait	No. of records	Mean	SD
Milk yield (kg)	23,966	5,017	1,281
Fat yield (kg)	23,863	226	53
Protein yield (kg)	23,406	185	43
Fat concentration (%)	23,813	4.55	0.59
Protein concentration (%)	23,389	3.66	0.25
SCS (log_{10} units)	23,284	5.0284	0.356

RESULTS

Milk Production

Mean milk yield, fat yield, protein yield, fat percentage, protein percentage, and geometric mean SCC for the population was 5,017 kg, 226 kg, 185 kg, 4.55%, 3.66%, and 133,397 cells/mL, respectively (Table 2). Milk volume yield was greatest for purebred Holstein cows, producing 12 and 19% more milk than their

Table 3. Number of records, mean and standard deviation estimates for reproduction traits across the population

Trait	No. of records	Mean	SD
Age at first calving (d)	4,249	736	50
Submission rate (%)	17,261	74	44
Calving to first service (d)	10,909	75	23
Calved within 42 d of calving season (%)	14,133	66	47
Calving interval (d)	18,244	379	58

purebred Friesian and Jersey contemporaries, respectively (Table 4). Similarly, milk solids yield (i.e., fat kg + protein kg) was greatest for purebred Holstein cows; milk solids yield of the Holstein cows was 9 kg (2%) greater than that of purebred Jersey cows and 43 kg (11%) greater than that of purebred Friesian cows (Table 4). Milk constituents (i.e., fat percentage and protein percentage) were 17.0 and 15.6% greater for purebred Jersey cows relative to their purebred Holstein and Friesian contemporaries, respectively (Table 4). Somatic cell count was least for purebred Friesian cows, 14.5% (13,960 cells/mL) and 8% (7,600 cells/mL) lower than that of purebred Holstein and purebred Jersey cows, respectively (Table 4).

Holstein × Jersey first-cross (F_1) cows produced more ($P < 0.001$) milk compared with the parental breed average (Table 4), equating to 264 kg (i.e., 5.6% heterosis) greater milk volume, 15 kg (i.e., 6.5% heterosis) greater milk fat yield, and 11 kg (i.e., 6.3% heterosis) greater milk protein yield. Somatic cell count was 8.6% (9,800 cells/mL) greater ($P < 0.001$) for Friesian × Jersey F_1 cows compared with the parental breed average (Table 4). Positive recombination effects were observed in multi-generational Holstein × Friesian cows, resulting in greater milk yield ($P < 0.001$), milk solids yield ($P < 0.001$), protein concentration ($P < 0.05$), and SCC ($P < 0.05$). Recombination effects for the other breed crosses were not different from zero except for the positive regression coefficient on fat concentration in Friesian × Jersey crosses (Table 4).

Reproductive Performance

Mean reproductive performance of the data set is in Table 2. There was no consistent breed effect on the different reproductive traits investigated. Purebred Friesian heifers calved 14 and 32 d younger ($P < 0.001$) than purebred Holstein and Jersey heifers, respectively (Table 5). The number of days from calving to first service was least for purebred Friesian cows, intermediate for purebred Jersey cows, and greatest for purebred Holstein cows (Table 5). Calving interval was shortest for purebred Friesian cows (376 d), intermediate for purebred Holstein cows (382 d), and longest for purebred Jersey cows (387 d) (Table 5). The proportion of cows served in the first 21 d of the breeding season was greatest for purebred Friesian cows, 6 and 14% greater than that of purebred Jersey and purebred Friesian cows, respectively (Table 5). The proportion of multiparous cows that calved in the first 42 d of the calving season was 13 and 16% greater for purebred Jersey cows compared with purebred Holstein and purebred Friesian cows, respectively (Table 5).

Table 4. Least squares means estimates (SE in parentheses) for Holstein (HO), Friesian (FR), and Jersey (JE) for milk production traits, and associated heterosis and recombination effects for each breed cross

	Breed			Heterosis			Recombination[1]		
Trait	HO	FR	JE	HO×FR	HO×JE	FR×JE	HO×FR	HO×JE	FR×JE
Milk yield (kg)	5,217[a]	4,591[b]	4,230[c]	45.0	263.8***	81.9	819.7***	22.6	624.6
	(31.2)	(93.2)	(43.5)	(91.8)	(41.8)	(90.7)	(123.4)	(147.4)	(333.0)
Fat yield (kg)	218[a]	193[b]	226[c]	5.2	14.5***	4.1	46.3***	4.9	22.5
	(1.3)	(3.8)	(1.8)	(3.7)	(1.7)	(3.7)	(5.0)	(6.0)	(13.6)
Protein yield (kg)	186[a]	168[b]	169[b]	0.6	11.1***	3.4	28.6***	2.9	20.3
	(1.1)	(3.1)	(1.5)	(3.1)	(1.4)	(3.0)	(4.1)	(5.0)	(11.2)
Fat %	4.22[a]	4.28[b]	5.42[c]	0.03	−0.04*	−0.05	0.02	0.01	0.05*
	(0.01)	(0.04)	(0.02)	(0.04)	(0.02)	(0.04)	(0.06)	(0.07)	(0.02)
Protein %	3.53[a]	3.63[b]	3.96[c]	−0.03	0.02	0.09	0.05*	0.05	−0.04
	(0.01)	(0.02)	(0.02)	(0.02)	(0.08)	(0.02)	(0.03)	(0.03)	(0.07)
SCS	5.0534[a]	4.9573[b]	5.0613[a]	0.4356	−0.1557	0.9053***	0.8383*	−0.8555	−0.7139
	(0.0093)	(0.0283)	(0.0129)	(0.2785)	(0.1226)	(0.2753)	(0.3721)	(0.4492)	(0.1023)

[a–c]Values within rows differing in superscript are different ($P < 0.05$).

[1]Regression coefficient on recombination coefficient.

*$P < 0.05$; ***$P < 0.001$: significance of difference from zero.

Table 5. Least squares means and predicted probability estimates (SE in parentheses) for Holstein (HO), Friesian (FR) and Jersey (JE) for fertility traits and associated heterosis and recombination effects for each breed cross

Trait[1]	Breed			Heterosis			Recombination[2]		
	HO	FR	JE	HO×FR	HO×JE	FR×JE	HO×FR	HO×JE	FR×JE
AFC (d)	744[a]	730[b]	762[c]	−1.3	−11.7***	−2.9	4.9	−18.4	−12.3
	(3.3)	(8.4)	(3.9)	(8.1)	(3.7)	(6.9)	(10.5)	(9.9)	(20.8)
CFS (d)	71.4[a]	68.9[b]	70.5[ab]	2.4	−0.4	−1.8	1.0	−3.2	12.0**
	(1.4)	(1.9)	(1.9)	(1.4)	(0.9)	(1.4)	(2.0)	(2.3)	(4.8)
CIV (d)	382[a]	376[b]	387[c]	−5.5	−7.6***	−9.3*	1.8	−16.7**	−2.6
	(1.7)	(4.6)	(2.7)	(4.3)	(2.1)	(4.2)	(5.9)	(7.1)	(15.9)
SR[3] (%)	68.1[a]	79.1[b]	74.4[b]	−4.55	3.17	0.88	1.29	4.82	−16.23*
	(1.9)	(4.1)	(2.7)	(−12.36 to 2.33)	(−0.19 to 6.26)	(−6.89 to 7.11)	(−4.05 to 6.13)	(−1.55 to 10.01)	(−35.86 to 0.29)
C42[3] (%)	66.0[a]	64.0[ab]	76.2[b]	3.31	−3.64	−9.46	3.90	−15.31	−16.71
	(5.4)	(11.0)	(6.6)	(−13.30 to 16.28)	(−14.09 to 5.33)	(−29.70 to 7.71)	(−8.48 to 13.65)	(−34.34 to 3.40)	(−49.35 to 22.19)

[a–c]Values within rows differing in superscript are different ($P < 0.05$).

[1]AFC = age at first calving, CFS = calving to first service, CIV = calving interval, SR = submission rate, C42 = calved within 42 d of calving season.

[2]Regression coefficient on coefficient of recombination for AFC, CFS, and CIV; for the binary traits, SR and C42, the recombination value presented is the expected performance of an offspring from the mating of 2 F_1 crossbred parents relative to the mean performance of those parents taking cognizance of differences in heterosis.

[3]Standard error for heterosis and recombination expressed as 95% CI.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Holstein × Jersey F_1 cows calved 12 d younger ($P < 0.001$) as heifers compared with the parental breed average (Table 5), corresponding to a 1.6% heterosis effect. Holstein × Jersey and Friesian × Jersey F_1 cows had an 8-d shorter (i.e., 2% heterosis; $P < 0.001$) and a 9-d shorter (i.e., 2.4% heterosis; $P < 0.05$) calving interval compared with the average of their respective parental breeds (Table 5). Holstein × Jersey backcrosses had a shorter ($P < 0.001$) calving interval compared with HO×JE first-cross cows due to favorable recombination effects.

DISCUSSION

Selection and crossbreeding in dairy cattle have almost always been studied separately and, with the exception of New Zealand, crossbreeding of dairy cattle has received limited acceptance worldwide (Buckley et al., 2014). Recent advances in genomic selection have accelerated the rate of genetic improvement in some cattle breeds (Spelman et al., 2013). Although beneficial aspects of crossbreeding are widely documented in the literature (Buckley et al., 2014), few studies have quantified the additional benefits of crossbreeding within commercial grass-based production systems, which are already intensively selected for grass-based production characteristics (Dillon et al., 2006). Hence, the objective of the current study was to compare the milk production and reproductive performance of Holstein, Friesian, and Jersey purebred cows with their respective crosses in commercial seasonal-calving, grass-based dairy herds.

Additive and Nonadditive Associations with Performance

Heterosis is defined as the increased performance of crossbred animals compared with the average of both purebred parental breeds (Sørensen et al., 2008) and is attributable to both inter- and intra-loci allelic interactions (Lopez-Villalobos et al., 2000c). Heterosis tends to be greater for crosses between more genetically diverse breeds (Cassell, 2007). Heterosis for production traits in dairy cows typically ranges from 0 to 10%, whereas heterosis for fertility traits in dairy cows typically ranges from 5 to 25% (Swan and Kinghorn, 1992; Buckley et al., 2014). The greatest level of heterosis in the present study was observed for the Holstein-Jersey F_1 cow, which was not unexpected because the 2 breeds were the most genetically diverse (Sørensen et al., 2008). Heterosis in the present study was least for the Holstein-Friesian F_1, 2 breeds that are genetically very similar (Sørensen et al., 2008).

The heterosis estimates of 5.6% for milk yield and 6.4% for milk solids observed in Holstein-Jersey F_1 cows in the present study is slightly larger than the estimates of 3.7 and 5.8% for milk yield and milk solids yield, respectively, in Holstein-Friesian × Jersey F_1 reported by Prendiville et al. (2011) in a smaller controlled study in Ireland.

Reproductive efficiency is fundamental to the profitability of seasonal-calving production systems and is underpinned by the ability of cows to resume cyclicity early postcalving, express estrus, conceive, and both establish and maintain pregnancy (Berry et al., 2014). Crossbreeding has been proposed as a method to rapidly reverse the decline in reproductive performance that occurred due to "holsteinization" (Buckley et al., 2014). Heterosis effects for reproductive performance in the present study were, however, lesser than heterosis estimates previously documented (Sørensen et al., 2008; Buckley et al., 2014). All crossbred cows in the present study had a shorter calving interval relative to the average of the parental breeds corresponding to 1.5, 2, and 2.4% heterosis for Holstein × Friesian, Holstein × Jersey, and Friesian × Jersey cows, respectively. The shorter calving interval observed for the Holstein × Jersey in the present study is consistent with previous research (Penasa et al., 2010) and is advantageous in seasonal milk production systems. Previous studies have also demonstrated superior reproductive performance in crossbred cows relative to parental purebreds, including a 22% greater in-calf rate to first service, a 19% greater in-calf rate after 6 wk of breeding, and an 8% greater in-calf rate after 13 wk of breeding (Prendiville et al., 2011; Vance et al., 2013).

Although first-cross cows generally perform favorably because of heterosis, performance in subsequent generations may be reduced due to the effects of recombination (Dechow et al., 2007). Recombination loss is defined as the disintegration of epistatic effects to form nonparent inter-loci combinations of alleles in crossbred animals (Cassady et al., 2002). Precise estimation of recombination effects, however, requires large numbers of second- and greater-generation crosses (Dechow et al., 2007) and the lack of significant recombination effects on milk production and fertility traits in Jersey backcross cows in the present study may be an artifact of the fewer multi-generational Jersey crossbred lactation records available (Table 1). In the present study, large but favorable recombination effects of 819.7 kg of milk and 74.9 kg of milk solids were detected in Holstein × Friesian backcrosses; however, the estimates were associated with large standard errors. Literature estimates of recombination effects for milk yield traits in dairy cattle are nonetheless variable but usually unfavorable, opposite to that observed in the present study. The previously reported recombination effects for milk yield have been reported to be between −232 kg (Brotherstone and Hill, 1994) and −135 kg (Akbas et al., 1993) in Holstein × Friesian crossbreds. Wall et al. (2005) also documented unfavorable recombination effects on test-day milk yield in Holstein × Friesian dairy cows, which actually exceeded the favorable heterosis effects in first-cross Holstein × Friesian cows from the same study population. In a meta-analysis of crossbred dairy cows, Lopez-Villalobos (1998) reported that recombination in multi-generational Friesian crossbreds can account for up to 80% of the heterosis effects for milk yield traits. Estimates of recombination for fertility traits in the present study were small but generally not different from zero. A favorable recombination effect was detected for calving interval in Holstein × Jersey backcross cows in the present study, consistent with that documented by Wall et al. (2005) in UK Holstein-Friesian dairy cows, although the latter estimates were not different from zero. Similarly, Dechow et al. (2007) reported a favorable, although not different from zero, recombination effect on days open, a trait similar to calving interval; recombination effects of Holstein-Montbéliarde and Holstein-Normande crosses (Dezetter et al., 2015) on calving to first service interval were +0.3 d and −4 d, respectively, but were associated with large standard errors, rendering them not different from zero. Thus, the effect of recombination appears, in most studies (except the present study), to have unfavorable consequences for milk production but possibly weak favorable effects on reproductive performance. This is not unexpected because recombination is expected to affect traits under selection, such as milk production, to a greater extent than traits not under long-term selection, such as reproductive performance (Sørensen et al., 2008). Different population breeding goals may therefore be one contributing factor to the inconsistencies among studies on the effect of recombination on different traits; greater natural selection pressure may have been traditionally placed on Irish dairy cows to survive within the seasonal calving production system operated in Ireland (Berry et al., 2013), which may have implied weaker selection pressure on milk production. Furthermore, Ireland traditionally did not operate its own national breeding scheme and therefore the germplasm used originated from many different sources, minimizing the potential for favorable epistatic loci combinations to become established (and therefore lost through continual crossbreeding).

In theory, with rotational crossbreeding between 2 breeds, 67% of the F_1 heterosis will be expressed (Sørensen et al., 2008; Buckley et al., 2014). Heterosis for 2-way rotational crosses in the present study exceeded theoretical expectations, where HO×JE rotational crosses expressed 70% and 100% of the heterosis observed in the HO×JE F_1 for milk solids and calving interval, respectively.

Economic Implications of Crossbreeding

The ideal cow for future milk production in Ireland has been characterized as a robust, healthy, efficient, fertile, easy-care cow that produces a large quantity of high-value milk solids and remains resilient to external perturbations (Berry, 2015). It is essential to incorporate all traits of interest into breeding indices to breed a fit-for-purpose cow suitable for a given production system. The breeding strategy in New Zealand demonstrates the best example of large-scale crossbreeding with the Jersey breed, where Holstein-Friesian × Jersey crossbred cows account for 42.6% of the national dairy herd (LIC, 2015). The appropriateness of Jersey crossbreeding in intensive grazing systems is substantiated by the results from the present study and elsewhere (Lopez-Villalobos et al., 2000a; Prendiville et al., 2009, 2011; Buckley et al., 2014) owing to high productivity of milk solids complementing the milk payment system, superior fertility performance, improved longevity, and consequently, an expected increase in overall farm profit.

The introduction of a multi-component milk payment system that rewards milk solids production and penalizes milk volume in many countries (Shalloo et al., 2007) has initiated a growing interest in crossbreeding. Based on the likely future milk pricing, as described by Kelleher et al. (2015a), where a kilogram of milk, fat, and protein is worth −€0.09, €1.04, and €6.64 profit, respectively, all F_1 crossbred cows in the present study generated more milk profit than the parental breed average (€67.12, €19.47, and €5.34 per lactation for Holstein × Jersey, Friesian × Jersey, and Holstein × Friesian F_1 cows, respectively). Similar trends were observed in New Zealand where Holstein-Friesian × Jersey cows produced 378 kg more milk and 28.7 kg more milk solids compared with the parental average (LIC, 2015), corresponding to €79 milk profit based on future milk pricing for Ireland (Kelleher et al., 2015a).

Based on the economic value of −€12.43 per day for calving interval in the Irish national breeding objectives (ICBF, 2014), the shorter calving interval in the present study was valued at €94.47, €115.60, and €68.37 extra profit per lactation for Holstein × Jersey, Friesian × Jersey, and Holstein × Friesian F_1 cows, respectively, compared with the parental breed average. Superior performance was also evident for age at first calving in the present study and, although no economic value is available for age at first calving in Ireland, this is also likely to contribute to overall profitability.

The economic benefits from superior milk production and reproductive performance in the present study equate to an additional €162, €135, and €74 profit per lactation for Holstein × Jersey, Friesian × Jersey, and Holstein × Friesian crossbred cows, respectively, relative to the parental breed average. This is consistent with previous economic analyses that attributed greater profitability to greater lifetime milk production, increased longevity, and lower replacement rates in crossbreds relative to their purebred contemporaries (Lopez-Villalobos et al., 2000a,b; Prendiville et al., 2011). Kelleher et al. (2015b) reported an additional €472 profit for Holstein × Jersey F_1 cows over their lifetime relative to the average of their purebred contemporaries.

Although not considered in the present study, crossbreeding has also been documented to contribute to superior health (Begley et al., 2009), feed efficiency (Grainger and Goddard, 2004; Prendiville et al., 2009), and longevity (Lopez-Villalobos et al., 2000a) in dairy cows. Because of improved milk composition, fertility, health, feed efficiency, and longevity observed in crossbred cows, an improvement in overall farm profitability is expected.

CONCLUSIONS

The findings from the present study corroborate previous conclusions from small-scale controlled experiments and illustrate the superior biological performance of crossbred cows relative to the average of parental breeds within seasonal-calving, grass-based commercial dairy herds. Moreover, the results indicate that the widespread adoption of crossbreeding offers the Irish dairy industry the opportunity to capitalize on heterosis for traits of economic importance and may result in a considerable improvement in profit. Consequently, to fully exploit crossbreeding and maximize attainable heterosis, high-genetic-merit bulls from complementary pure breeds must be available to dairy farmers.

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