Effects of Breed and Feeding System on Milk Production, Body Weight, Body Condition Score, Reproductive Performance, and Postpartum Ovarian Function

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ABSTRACT

The objective of this study was to investigate the potential differences among Holstein-Friesian (HF), Montbéliarde (MB), Normande (NM), Norwegian Red (NRF), Montbéliarde × Holstein-Friesian (MBX), and Normande × Holstein-Friesian (NMX) across 2 seasonal grass-based systems of milk production. The effects of breed and feeding system on milk production, body weight, body condition score, fertility performance, hormone parameters, ovarian function, and survival were determined by using mixed model methodology, generalized linear models, and survival analysis. The 5-yr study comprised up to 749 lactations on 309 cows in one research herd. The HF produced the greatest yield of solids-corrected milk, the MB and NM produced the least yields, and NRF, MBX, and NMX were intermediate. The NRF had the lowest body weight throughout lactation, the NM had the highest, and the other breeds were intermediate. Body condition score was greatest for MB and NM, least for HF, and intermediate for NRF, MBX, and NMX. The HF had a lower submission rate and overall pregnancy rate compared with the NRF. The NRF survived the longest in the herd, the HF survived the shortest, and the NM, MB, MBX, and NMX were intermediate. Breed of dairy cow had no effect on selected milk progesterone parameters from 5 d postpartum until 26 d after first artificial insemination. Breed of dairy cow did not influence insulin and insulin-like growth factor-1 around parturition or at the start of the breeding season. Animals offered a high-concentrate diet had greater milk yield, but they did not have improved reproductive performance. Differences observed between the different breeds in this study are a likely consequence of the past selection criteria for the respective breeds.

Key words: dairy, milk production, reproductive performance, breed

INTRODUCTION

Achieving high reproductive efficiency is fundamental to profitability across all dairy production systems. In seasonal grass-based dairy systems such as in Ireland, the relative importance of fertility is greater than in confinement and year-round calving systems, because breeding and calving are restricted to a limited period of the year (Veerkamp et al., 2002). The rationale for this strategy is to obtain a concentrated calving pattern in spring (February to April) that enables grass growth to match food demand. This is achieved by attaining high pregnancy rates within a short interval after the start of the breeding season. Calving intervals of 365 to 370 d and a culling rate for infertility of less than 10% are required for optimal financial performance within a seasonal dairy system (Esslemont et al., 2001). Increased genetic merit for milk production (Buckley et al., 2000a), introgression of Holstein-Friesian (HF) genes (Evans et al., 2006), and increased negative energy balance during early lactation (Butler, 2003) have been cited as major factors contributing to declining fertility. Various dietary strategies have been used in an attempt to resolve body lipid mobilization nutritionally (Gong et al., 2002). More recently, there has been increasing emphasis on genetics as a solution, either within breed, between breeds, or by crossbreeding (Dillon et al., 2003b; Heins et al., 2006b). Many of the leading dairy countries have incorporated fertility traits into national genetic evaluation systems in an attempt to resolve the decline in reproductive performance (Miglior et al., 2005).

Genetic selection programs based solely on increasing milk production have resulted in cows that are genetically predisposed to a greater risk of dietary energy deficit, particularly in the early lactation period. The correlated response in DMI to selection for milk yield is approximately half (Veerkamp et al., 1994); therefore, increases in feed intake only partially offset the extra energy demands for milk yield, resulting in a greater degree of body tissue mobilization. Body condition score has been shown to be both phenotypically (Buck-

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ley et al., 2003) and genetically (Berry et al., 2003a) associated with reproductive performance. Cows that are genetically superior milk producers tend to have genetically lower BCS throughout lactation (Dechow et al., 2001) and have a greater BCS change in early lactation than those of lower genetic merit (Grainger et al., 1985; Buckley et al., 2000b).

Accepted measures of fertility, such as the interval from calving to first service and submission rates, are greatly influenced by management decisions; thus, these parameters may not be a true reflection of innate fertility performance. Royal et al. (2002) reported heritability estimates of 0.13 to 0.17 for different milk progesterone parameters and unfavorable additive genetic correlations between these parameters with milk yield. Phenotypically, the interval to first service increased as the interval to commencement of luteal activity increased (Royal et al., 2002). Thus, it has been suggested that the interval from calving to commencement of luteal activity be incorporated in a selection index as an indicator of reproductive efficiency (Darwash et al., 1997; Royal et al., 2002). Insulin and IGF-1 concentrations are lower in animals genetically selected for increased milk yield (Snijders et al., 2000). This can result in impaired ovarian follicular development, thus compromising reproductive efficiency (Butler, 2003). Results from Gong et al. (2002) showed a marked reduction in the interval from calving to first ovulation in dairy cows selected for both high and low genetic merit milk production that were fed a diet promoting greater insulin release in response to feeding.

Results from Scandinavia, where fertility has been included in genetic selection programs since the 1970s, illustrate that it is possible to select for improved fertility (Andersen-Ranberg et al., 2003) because sufficient additive genetic variation exists within fertility traits (Pryce and Veerkamp, 2001). In France, the Montbéliarde (MB) and Normande (NM) breeds have been simultaneously selected for both milk and beef production. Interest in the potential use of alternative breeds and crossbreeding has increased as a means of improving economic efficiency through their perceived superior functionality compared with the HF (Heins et al., 2006a,b). The current study provides a unique opportunity to investigate the 5-yr reproductive performance data of 6 different dairy cow genotypes, managed as a single herd, across 2 pasture-based feeding systems. Previous results using the same data set highlight superior udder health with the MB and Norwegian Red (NRF; Walsh et al., 2007). Therefore, the objective of this study was to investigate the reproductive performance among HF, MB, NM, NRF, MB $\times$ HF (MBX), and NM $\times$ HF (NMX) across 2 seasonal grass-based systems of milk production.

MATERIALS AND METHODS

Genotypes and Feeding Systems

A 5-yr study to compare HF, MB, NM, NRF, MBX, and NMX took place on the Ballydague Dairy Research Farm at Moorepark Dairy Research Centre, Ireland, from January 2001 through December 2005. This study was a continuation of a breed comparison trial described by Dillon et al. (2003a) and detailed further by Walsh et al. (2007).

Briefly, purebred MB and NM cows were available on completion of a 5-yr comparison of Dutch HF, MB, NM, and Irish HF. In 1999, NRF calves were imported and reared with the other breeds. Crossbreds and HF were generated by randomly mating HF, MB, and NM sires to HF cows from herds within Moorepark Dairy Research Centre. Replacement animals were generated within the herd during the 5 yr. A total of 23, 19, 17, 11, 19, and 17 sires were represented in the HF, MB, MBX, NM, NMX, and NRF breeds, respectively. Sires used were common across pure and crossbreds and were also representative of sires commonly used in Ireland. The HF sires used were of North American HF ancestry. The average number of HF, MB, MBX, NM, NMX, and NRF per year over the 5 yr of the study was 33, 27, 28, 14, 20, and 30, respectively. The average lactation number was 1.1, 1.7, 2.3, 2.7, and 2.9 for yr 1, 2, 3, 4, and 5. Breed groups were not balanced for parity (1, 2, 3, 4, or 5) or calving date.

Throughout the 5 yr, the trial was carried out on the same permanent grassland site consisting of a perennial ryegrass sward and is detailed by Walsh et al. (2007). Briefly, cows were at pasture from mid-February until late November each year. Cows were housed during the winter months and were dry for the most part during this time. First-lactation animals were allocated a 10-wk dry period, whereas an 8-wk dry period was considered sufficient for multiparous animals. Postpartum and before turnout to pasture, grass silage ad libitum and 6 kg of concentrates were offered daily. Once at pasture, cows received 4 kg of concentrates daily. Each year of the study, calving date and milk yield were used as criteria to group cows into blocks of 2 within breed groups in mid- to late April. The breed groups were then randomized across 2 spring-calving grass-based feeding systems, a low-concentrate feeding system (LC) and high-concentrate feeding system (HC). Those on the HC feeding system were offered 4 kg/cow daily postrandomization (approximately 1,030 kg/cow for total lactation), whereas those on the LC feeding system were not offered concentrate supplementation postrandomization (approximately 530 kg/cow for the total lactation). Concentrates were offered on a flat

rate basis and were fed in individual stalls twice daily at milking time.

Reproductive Management

Each year, a 13-wk breeding season was imposed, beginning in late April and finishing in late July. Heat detection commenced immediately postpartum and involved monitoring the cows for expressions of estrus at morning milking, at noon, and at evening milking until the end of the breeding season. Detection of estrus was facilitated by the use of tail paint. Artificial insemination was performed by an experienced professional AI technician each year. Semen was examined before the breeding season to ensure the use of semen with good sperm motility as well as with a high proportion of live sperm. Only sires found to have semen with greater than 50% sperm motility and greater than 60% of live sperm were used in AI. The average motility and proportion of live sperm present in the semen used did not differ between breeds. Cows observed in estrus in the morning were inseminated that morning, whereas those first observed at noon and at the evening milking were inseminated the following morning. Pregnancy diagnosis was determined by using transrectal ultrasound imaging (Aloka SDD 500V scanner with a 5-MHz transducer, Aloka Ltd., Tokyo, Japan) 6 wk after the end of the defined breeding season.

Animal Measurements

Milk Yield and Composition. A total of 31,167 weekly records from 749 lactations of 309 cows were included in the analysis for milk production. The data were restricted to between 5 and 305 DIM. Individual cow milk yield was recorded daily by using electronic milk meters (Dairymaster, Causeway, Co. Kerry, Ireland). Milk samples, collected once weekly from successive morning and evening milkings, were analyzed by using a MilkoScan 203 instrument (Foss Electric, Hillerød, Denmark) to determine milk fat, protein, and lactose concentrations. Solids-corrected milk yield was calculated by using the equation of Tyrrell and Reid (1965), where $SCM\ (kg) = 12.3\ fat\ (kg) + 6.56 \times SNF\ (kg) - 0.0752 \times milk\ yield\ (kg)$.

BCS and Live Weight. A total of 8,207 BCS and 39,743 live weight (BW) records of 309 cows were analyzed. Cow BCS and BW were categorized into 10 stages of 4 wk each, with the last stage being wk 37 to 44. Average weekly BW was calculated within these 10 stages. Cow BCS was recorded every 3 to 4 wk by the same experienced classifier during the lactation on a 1 to 5 scale (1 = emaciated, 5 = extremely fat) with increments of 0.25 (Lowman et al., 1976). Cow BW was

recorded once weekly by using calibrated electronic weighing scales (Dairymaster).

Fertility Traits. A total of 309 cows were included in the analysis of fertility traits. Eight fertility traits reflecting phenotypic fertility performance were investigated and were analyzed per breed group. These included calving day of year, 24-d submission rate (**SR24**; proportion of all cows detected in estrus and submitted for AI in the first 24 d of the breeding season), calving to first service (**CTFS**; interval from calving to first service), pregnancy rate to first service (**PREG1**; proportion of all cows confirmed pregnant 6 wk after the end of the breeding season, to first AI), 6 wk in calf rate (**PREG42**; proportion of all cows confirmed pregnant 6 wk after the end of the breeding season, to an insemination occurring within 6 wk after the start of the breeding season), overall pregnancy rate (**FINALPR**; proportion of all cows confirmed pregnant 6 wk after the end of the breeding season), calving to conception interval (**DO**; days from calving to confirmed pregnancy diagnosis 6 wk after the end of the breeding season), and finally, number of services per cow (total number of services divided by the total number of cows).

Milk Progesterone. During yr 3 and 4 of the study, composite milk samples were obtained 3 times weekly on Mondays, Wednesdays, and Fridays during the morning milking. Commencement of sampling began 5 d postpartum and extended to 26 d after first AI. A potassium dichromate preservative tablet (Lactab Mark III, Thompson & Capper Ltd., Cheshire, UK) was added to each milk sample, and all samples were stored at 4°C until assayed for progesterone. Whole-milk progesterone was measured by enzyme immunoassay (Ridgeway Science Ltd., Gloucestershire, UK) as outlined by Sauer et al. (1986). Inter- and intraassay coefficients of variation were 13.7 and 15.7%, respectively. The sensitivity, calculated by using the absorption of the blank standard – 2 standard deviations, was 0.5 ng/mL.

Data from 187 cows were included for the progesterone parameter analysis, taking note of repeated measures for these cows. Milk progesterone profile parameters were defined as outlined by Royal et al. (2000) and Horan et al. (2005b). The 3 times weekly milk sampling protocol introduced sampling bias to some parameters; hence, these were adjusted for accordingly (Royal et al., 2000).

Commencement of Luteal Activity Postpartum. The commencement of luteal activity (**CLA**) was defined as the interval from calving until the first of 2 or more consecutive milk progesterone concentrations of ≥ 3 ng/mL (Royal et al., 2000).

Luteal Phase. The luteal phase (**LP**) is the period after ovulation in which a corpus luteum secretes progesterone measuring ≥ 3 ng/mL in milk (Royal et

al., 2000). The number of days between the first consecutive milk sample ≥ 3 ng/mL (time T_1) and the final consecutive milk sample of ≥ 3 ng/mL (time T_2) is the length of the LP.

Interovulatory Interval. This measure is regarded as an objective measure of estrous cycle length (Royal et al., 2000) and is defined as the interval between commencement of one LP to the commencement of the subsequent LP, as outlined above.

Interval Between CLA and First AI. This is the interval from the initiation of the first LP postpartum to the day of first insemination (Royal et al., 2000).

Interluteal Interval. The interluteal interval (ILI) refers to the interval in days between the demise of one corpus luteum and the appearance of the next (Royal et al., 2000). The first milk sample of < 3 ng/mL after luteolysis until the last consecutive milk sample < 3 ng/mL is the ILI.

Atypical Ovarian Hormone Patterns. Four types of progesterone profiles were classified as abnormal and defined in accordance with Royal et al. (2000): 1) delayed ovulation type I is characterized by milk progesterone concentration of < 3 ng/mL for a period of ≥ 45 d postpartum; 2) delayed ovulation type II is characterized by an ILI of ≥ 12 d postpartum; 3) persistent corpus luteum type I is defined as milk progesterone concentrations of ≥ 3 ng/mL for ≥ 19 d during the first LP postpartum; and 4) persistent corpus luteum type II is distinguished by milk progesterone concentrations of ≥ 3 ng/mL for ≥ 19 d during the second and subsequent LP postpartum.

Insulin and IGF-1. A total of 556 samples were available for analysis: 131 precalving, 145 within 1 wk of calving, 118 postcalving, and 111 at the start of the breeding season. The average number of days for precalving, calving, postcalving, and at the start of the breeding season was -4, 5, 36, and 53, respectively. Plasma IGF-1 concentrations were determined by using a validated double-antibody RIA after ethanol-acetone-acetic acid extraction. The standard and iodinated tracer used was recombinant human IGF-1 (R&D Systems Europe, Abingdon, UK). Iodine-125 (PerkinElmer; Unitech BD Ltd., Dublin, Ireland) was used for the iodination. The extraction and assay were carried out as described by Echternkamp et al. (1990). Inter- and intraassay coefficients of variation were 21.5 and 16.6%, respectively. Plasma insulin concentrations were determined by using a solid-phase fluoroimmunoassay (AutoDELFIA, PerkinElmer Life and Analytical Science, Turku, Finland). The plasma insulin data were not normally distributed; hence, plasma insulin data were log-transformed (natural logarithm) before statistical analysis. The inter- and intraassay coefficients of variation were 14.8 and 3.7%, respectively.

Statistical Analysis

Mixed Model Analysis. Milk production, BW, BCS, number of services per cow, CTFS, and DO were analyzed by using a repeated measures model in PROC MIXED (SAS Institute, 2006). Cow was included as a random effect, whereas breed, feeding system, parity, and year were included as fixed effects. Calving day of year was included as a quadratic effect. Specifically for milk production variables, BCS, and BW, a preexperimental covariate was created to adjust for differences that may have existed in preexperimental performance (bias). The covariate was created by using the mean of the 2-wk performances immediately before the feeding treatments were applied. The covariate was centered (with a mean of 0) within breed group and lactation number before inclusion in the models. For analysis of BW and BCS on a per-stage of lactation basis, stage of lactation was included as a repeated effect within cow-lactation, and cow was included as a random effect. Breed, feeding system, parity, and year were included as fixed effects. The interaction between breed and lactation stage was also investigated.

All progesterone parameters and insulin and IGF-1 concentrations taken at the 4 time points were analyzed, with cow included as a repeated effect and breed, parity, DIM, and calving day of year included as fixed effects. Feeding system was not applied during the sampling time frame, and hence was not included in the model.

Selection of the covariance structure was based on minimization of the Akaike information criterion value. An unstructured correlation structure, compound symmetry, first-order autoregressive, and heterogeneous first-order autoregressive correlation structure were tested. These correlation structures account for the repeated measures within cow. Interactions between independent variables were also investigated. Evidence of heterosis was tested by using the CONTRAST/ESTIMATE statements (SAS Institute, 2006) where appropriate.

Generalized Linear Models. Analysis of SR24, PREG1, PREG42, and FINALPR was undertaken by using PROC GENMOD (SAS Institute, 2006), assuming a logit link function. Cow was included as a repeated effect, with an exchangeable correlation structure assumed between records within cow. The odds ratios were calculated as the exponent of the associated model solution for that variable. Empirical model solutions and standard errors are reported. Fixed effects included in the model were breed, feeding system, parity, and year, with calving day of year included as a continuous covariate. The HF and LC feeding systems were designated the reference groups [odds ratio (OR)

= 1] when determining the effect of breed and feeding system, respectively. Interactions between independent variables were also investigated.

Survival Analysis. Data from 293 cows that entered the study in their first lactation were included in the survival analysis. Survival was measured as the number of days from first calving to the date of culling. Date of culling for infertility was defined as the date of drying off at the end of lactation during which the cow failed to conceive. Culling date for reasons other than fertility was defined as the date on which the animal was removed from the herd. Animals that were pregnant on the last day of 2005 were assumed censored because their survival time was unknown (146 cows). The effect of breed on cow survival was analyzed by the Cox proportional hazards model by using PROC PHREG of SAS. Kaplan-Meier survival functions were estimated for each breed by using PROC LIFETEST in SAS.

RESULTS

Milk Production

The interaction between breed and feeding system was not significant for total milk production; therefore, Table 1 presents only the main effects. Breed of dairy cow influenced ($P < 0.05$) all milk yield variables, with the exception of protein percentage. Compared with the MB (5,604 kg) and NM (5,464 kg), all other breeds had greater total lactation milk yield ($P < 0.05$), with the HF having the greatest (5,925 kg). The SCM yield of the HF (5,467 kg) was greater ($P < 0.001$) than the MB (5,125 kg), NM (5,044 kg), and NRF (5,278 kg), but was similar to the MBX (5,332 kg) and NMX (5,382 kg). The HF produced more fat (226 kg), protein (202 kg), and lactose (279 kg) over the lactation ($P < 0.01$) compared with both the MB (207, 193, 266 kg, respectively) and the NM (204, 188, 260 kg, respectively). The NRF had similar fat (216 kg), protein (198 kg), and lactose (270 kg) yields compared with the MBX (219, 198, 274 kg, respectively) and NMX (222, 198, 275 kg, respectively). Compared with the HF (3.83%), fat percentage was similar for the NM (3.80%), MBX (3.78%), and NMX (3.91%), greater than that of the MB (3.71%) and NRF (3.72%). Lactose percentage of the MB (4.76%) and NM (4.78%) was greater ($P < 0.05$) compared with all other breeds, with the exception of the NRF (4.75%). Heterosis estimates for milk yield, SCM, and fat, protein, and lactose yields for the MBX were 0.4, 0.7, 0.9, 0.3, and 0.8% respectively, whereas for the NMX these were 2.3, 3.2, 4.4, 2.0, and 2.5% respectively.

Animals offered an HC diet achieved greater milk yield (5,840 kg); SCM (5,380 kg); fat (220 kg), protein (200 kg), and lactose yields (276 kg); and lactose per-

Table 1. Effect of breed of dairy cow¹ and feeding system² on milk production over the complete lactation

Variable	Breed						Feed system					
	HF	MB	NM	NRF	MBX	NMX	SEM	P-value	HC	LC	SEM ³	P-value
Milk yield (kg/cow)	5,925 ^a	5,604 ^b	5,464 ^b	5,788 ^a	5,789 ^a	5,795 ^a	70.7	<0.001	5,840	5,614	47.1	<0.001
SCM yield (kg/cow)	5,467 ^a	5,125 ^b	5,044 ^b	5,278 ^c	5,332 ^{ac}	5,382 ^{ac}	62.4	<0.001	5,380	5,163	42.0	<0.001
Fat yield (kg/cow)	226 ^a	207 ^b	204 ^b	216 ^c	219 ^c	222 ^{ac}	2.8	<0.001	220	211	1.9	<0.001
Protein yield (kg/cow)	202 ^a	193 ^{bc}	188 ^b	198 ^a	198 ^a	198 ^{ab}	2.3	<0.001	200	193	1.5	<0.001
Lactose yield (kg/cow)	279 ^a	266 ^{bc}	260 ^b	270 ^c	274 ^{ac}	275 ^{ac}	3.4	<0.01	276	265	2.3	<0.001
Milk composition (g/kg)												
Fat	38.3 ^{ad}	37.1 ^{bc}	38.0 ^{acd}	37.2 ^{bc}	37.8 ^{ac}	39.1 ^d	0.36	<0.001	37.8	38.0	0.21	NS
Protein	34.0	34.2	34.5	33.9	34.0	34.3	0.18	NS	34.2	34.1	0.11	NS
Lactose	47.0 ^a	47.6 ^b	47.8 ^b	46.7 ^d	47.3 ^c	47.5 ^{bc}	0.11	<0.001	47.4	47.2	0.07	<0.01

^{a-d}Means within a row with different superscripts differ ($P < 0.05$).

¹HF = Holstein-Friesian; MB = Montbéliarde; NM = Normande; NRF = Norwegian Red; MBX = Montbéliarde × Holstein-Friesian; NMX = Normande × Holstein Friesian.

²HC = high-concentrate feeding system; LC = low-concentrate feeding system.

³SEM = pooled SEM.

centage (4.74%) compared with those on the LC feeding system (5,614; 5,163; 211, 193, 265 kg; and 4.72%, respectively). Fat and protein percentages did not differ between feeding systems.

BCS and Live Weight

Breed and feeding system influenced both lactation average BCS and BW ($P < 0.001$). Compared with all breeds, the lactation average BCS of the HF was lower (2.77 BCS; $P < 0.001$). The lactation average BCS of the MB and NM were similar at 3.15 and 3.16, respectively, whereas the MBX, NMX, and NRF were similar at 3.00, 3.00, and 3.06, respectively. Lactation average BW was lower for NRF (537 kg; $P < 0.001$) compared with all breeds. The NM had the greatest lactation average BW (587 kg; $P < 0.05$) compared with all breeds (HF = 570 kg; MB = 568 kg; MBX = 572 kg), whereas BW of the NMX was similar (575 kg).

The interaction between stage of lactation and breed was significant for BCS ($P < 0.001$) and BW ($P < 0.001$) and is detailed in Figure 1. All breeds lost BCS immediately postpartum. Body condition score loss from wk 2 to 8 was greatest in the NRF (−0.19 BCS) and the HF (−0.15 BCS), was smallest in the MB and NM (−0.09 BCS), and for the MBX and NM was intermediate (−0.11 BCS). At each stage of lactation, the HF had lower BCS ($P < 0.001$) compared with all breeds. Between wk 29 and 44, all breeds began to regain body condition and reach values that were observed previously in wk 5 to 8 of lactation. The lowest BW throughout lactation was observed for the NRF ($P < 0.001$), whereas numerically greater BW was observed for the NM at each stage of lactation compared with all other breeds.

An interaction between stage of lactation and feeding system was also observed for BCS ($P < 0.001$) and BW ($P < 0.001$; Figure 2). Animals in both feeding systems had similar BCS from wk 2 to 12 (feeding system not applied from wk 2 to 8); thereafter, animals on the HC feeding system achieved greater BCS (approximately 0.1 BCS) for the remainder of the lactation ($P < 0.001$). Similarly for BW, feeding system influenced the lactation profile from wk 13 to 44 ($P < 0.001$), with those animals on the HC diet achieving greater BW from mid- to late lactation (approximately 10 kg heavier).

Reproductive Efficiency

The interaction between breed and feeding system was not significant for the 7 fertility parameters investigated, and hence was omitted from the analysis. On average over the 5 yr of the study, the MB had a later calving day of year ($P < 0.05$) compared with all other breeds (Table 2). Compared with the HF, the CTFS was shorter ($P < 0.05$) for the NM, NRF, and

MBX, whereas the CTFS of the MB and NMX was not different. The MB had a later DO compared with all other breeds, with the exception of the HF ($P < 0.05$). The number of services per conception during the defined breeding season did not differ between the breeds. Table 3 shows the association between breed of dairy cow and feeding system, with the probability of SR24, PREG1, PREG42, and FINALPR. The NRF (OR = 2.49) and MBX (OR = 3.11) had an increased probability of SR24 ($P < 0.05$) compared with the HF (Table 3). This corresponds to SR24 of 89, 91, and 76% for the NRF, MBX, and HF, respectively. The NRF (OR = 1.57) and NMX (OR = 1.62) tended to have a greater, but not statistically significant, PREG1 compared with the HF. Corresponding PREG1 rates for the HF, MB, NM, NRF, MBX, and NMX were 46, 39, 52, 57, 46, and 58%, respectively. The PREG42 was greater in the NM (OR = 1.80; $P < 0.05$) and also tended to be greater, but not statistically significant, in the NRF (OR = 1.56; $P = 0.074$) compared with the HF. Compared with the HF, the MB (1.99), NRF (2.48), MBX (2.40), and NMX (2.37) had a greater probability of FINALPR at the end of the breeding season ($P < 0.05$). Corresponding FINALPR rates for the HF, MB, NM, NRF, MBX, and NMX were 80, 89, 87, 91, 90, and 90%, respectively.

Animals offered an LC diet required fewer services per conception ($P < 0.05$) compared with those on the HC feeding system. The probability of PREG1 was greater for those animals offered an LC diet (OR = 1.41; $P < 0.05$) and also tended to be greater, but not statistically significant, for FINALPR (OR = 1.51; $P = 0.086$) compared with the HC feeding system.

Milk Progesterone, Insulin, and IGF-1

Breed of dairy cow did not influence any of the postpartum luteal activity profiles studied. However, the effect of breed on the first LP and average LP length tended toward significance ($P = 0.069$ and $P = 0.069$, respectively). The HF had the longest, and the NRF had the shortest, first LP and average LP length. The mean CLA across all breeds for the 2 yr was 31.3 d (SD 13.78), ranging from 29.4 d for the MBX to 33.8 d for the NRF.

Neither insulin nor IGF-1 concentrations were influenced by breed at any sampling period (Table 4). However, insulin and IGF-1 concentrations were different ($P < 0.001$) over time. Feed system did not influence milk progesterone, insulin, and IGF-1 concentrations.

Survival

Survival function curves are presented in Figure 3. Age at first calving for the HF, MB, NM, NRF, MBX,

Figure 1. Effect of Holstein-Friesian (●), Montbéliarde (■), Normande (▲), Norwegian Red (○), Montbéliarde × Holstein-Friesian (□), and Normande × Holstein-Friesian (▲) on BCS and live weight across different stages of lactation. Vertical bars indicate one pooled standard error.

and NMX was 751 d (SD 54.9), 765 d (SD 105.0), 741 d (SD 76.7), 730 d (SD 29.1), 727 d (SD 37.3), and 724.5 d (SD 29.1), respectively. Median survival days post first calving for the HF, MB, NM, NRF, MBX, and NMX were 695 (1.9 lactations), 1,023 (2.8 lactations), 1,068 (2.9 lactations), 1,416 (3.9 lactations), 1,385 (3.8 lactations), and 1,171 (3.2 lactations), respectively. The distribution of the number of survival days was skewed and was different for the different breeds and the crossbreds. Compared with the HF, the NR ($P < 0.01$), MBX ($P < 0.05$), and NMX ($P = 0.0862$) were more likely to remain in the herd longer. However, the longevity of the MB and NM was not different from that of the HF.

DISCUSSION

Until recently, many breeding programs placed the most emphasis on milk production, without concern

for functional traits (e.g., fertility, SCC). Intense genetic selection for milk yield has predisposed animals to increased negative energy balance, greater disease susceptibility (Pryce and Veerkamp, 2001), and decreased fertility (Veerkamp et al., 2003). The current study provided a unique opportunity to investigate the performance of different dairy cow breeds selected with very different breeding objectives across 2 pasture-based feeding systems.

The US breeding program has exerted considerable influence on dairy cow populations internationally because of the replacement of native genotypes with North American Holsteins (Evans et al., 2006; Gandini et al., 2007). Consequently, the rate of genetic gain in milk volume per cow per year since 1985 has been 193, 131, 35, and 46 kg, for the United States, the Netherlands, New Zealand, and Ireland, respectively (Dillon et al., 2006). In the current study, the superior

Table 2. Effect of breed of dairy cow¹ and feeding system² on calving day of year (CALDOY), calving to first service interval (CTFS; days), calving to conception interval (DO; days), and the number of services per conception (SERNO)

Variable	Breed							<i>P</i> -value	Feed system			
	HF	MB	NM	NRF	MBX	NMX	SEM ³		HC	LC	SEM	<i>P</i> -value
CALDOY	50 ^a	62 ^b	54 ^a	49 ^a	52 ^a	53 ^a	2.3	<0.001	54	52	1.3	NS
CTFS	73.3 ^a	71.8 ^{ac}	68.9 ^{bc}	70.1 ^{bc}	68.2 ^{bd}	71.3 ^{acd}	1.28	<0.05	70.3	70.9	0.82	NS
DO	89.9 ^{ab}	95.3 ^b	83.6 ^a	85.4 ^a	86.7 ^a	87.9 ^a	2.46	<0.05	89.3	86.9	1.62	NS
SERVNO	1.98	2.05	1.89	1.82	1.97	1.83	0.105	NS	2.01	1.83	0.068	<0.05

^{a-d}Means within a row with different superscripts differ ($P < 0.05$).

¹HF = Holstein-Friesian; MB = Montbéliarde; NM = Normande; NRF = Norwegian Red; MBX = Montbéliarde × Holstein-Friesian; NMX = Normande × Holstein Friesian.

²HC = high-concentrate feeding system; LC = low-concentrate feeding system.

³SEM is the average SEM.

Figure 2. Effect of the high-concentrate feeding system (●) and low-concentrate feeding system (▲) on BCS (units) and live weight (kg) across different stages of lactation. Vertical bars indicate one pooled standard error.

Table 3. Estimated odds ratios (OR) and their 95% confidence intervals (CI) for the effect of breed¹ and feeding system² on 24-d submission rate (SR24), pregnancy rate to first service (PREG1), 6-wk in-calf rate (PREG42), and overall pregnancy rate (FINALPR)

Variable	OR ¹	95% CI ²	P-value
Probability of SR24			
Breed			
HF	1		
MB	1.78	0.92–3.42	0.085
NM	1.92	0.79–4.69	0.152
NRF	2.49	1.20–5.17	0.014
MBX	3.11	1.47–6.57	0.003
NMX	1.92	0.82–4.50	0.131
Feeding system			
HC	1		
LC	0.92	0.57–1.47	0.727
Probability of PREG1			
Breed			
HF	1		
MB	0.75	0.44–1.27	0.287
NM	1.28	0.77–2.13	0.349
NRF	1.57	0.97–2.52	0.064
MBX	1.03	0.62–1.73	0.902
NMX	1.62	0.98–2.71	0.062
Feeding system			
HC	1		
LC	1.41	1.04–1.92	0.027
Probability of PREG42			
Breed			
HF	1		
MB	0.91	0.54–1.55	0.737
NM	1.80	1.08–3.00	0.025
NRF	1.56	0.96–2.55	0.074
MBX	1.43	0.85–2.41	0.183
NMX	1.34	0.78–2.29	0.288
Feeding system			
HC	1		
LC	1.31	0.94–1.82	0.115
Probability of FINALPR			
Breed			
HF	1		
MB	1.99	1.04–3.82	0.039
NM	1.72	0.77–3.85	0.185
NRF	2.48	1.23–4.97	0.011
MBX	2.40	1.20–4.80	0.013
NMX	2.37	1.10–5.08	0.027
Feeding system			
HC	1		
LC	1.51	0.94–2.41	0.086

¹HF = Holstein-Friesian; MB = Montbéliarde; NM = Normande; NRF = Norwegian Red; MBX = Montbéliarde × Holstein-Friesian; NMX = Normande × Holstein-Friesian.

²HC = high-concentrate feeding system; LC = low-concentrate feeding system.

milk production of the HF relative to the other breeds reflects the greater emphasis on milk yield in the breeding program from which it originates and agrees with the report of Dillon et al. (2003a). Although the Norwegian breeding program has encompassed a wide range of traits since the 1970s, milk production had been the most important trait in their breeding objective until 1997 (Andersen-Ranberg et al., 1998). Average milk yield per cow per year increased from 5,428

kg in 1975 to 6,605 kg in 2005 in Norway (Østerås et al., 2007). Cumulative milk yield of the NRF in this study did not differ from that of the HF. The superior milk production of the HF compared with the MBX and NMX in this study corroborates the findings of Heins et al. (2006a), who reported lower milk, fat, protein, and lactose yields for the MBX and NMX. In the current study, milk production of the crossbreds was greater than that for the MB and NM.

Milk production for the HF, MB, NM, and NRF in the current study was lower than previously reported from their country of origin (Sigwald and Dervishi, 2002; Heins et al., 2006a; Østerås et al., 2007). This is primarily a result of the pasture-based feeding systems used in the study. However, Horan et al. (2005a) demonstrated that cows with high genetic merit have a greater milk yield response to concentrate supplementation within a pasture system, resulting in a genotype × environment interaction for milk production. The current study did not identify any genotype × environment interaction for milk production. The difference in concentrate supplementation between the feeding systems imposed by Horan et al. (2005a) was greater than that for the current study (approximately 1,100 vs. 500 kg, respectively). Therefore, differences between the feeding systems tested in the current study may not have been sufficient to elicit a genotype × environment interaction.

Previous studies have highlighted the negative correlations between BCS and BCS change with milk yield (Buckley et al., 2000b; Berry et al., 2003b). Similarly, differences between breeds in their ability to partition energy toward milk production and body reserves have also been reported (Dillon et al., 2003a; Yan et al., 2006). Mean BCS for the NRF was similar to that reported by Yan et al. (2006) and BCS for the NRF in both studies was greater than that of HF contemporaries. In early lactation, BCS loss was similar for the HF and NRF; however, because of differences in precalving BCS, the HF reached a lower BCS nadir. Furthermore, in mid- to late lactation, the NRF showed a greater propensity to gain BCS than the HF, thus replenishing more body condition for the subsequent lactation. This supports the hypothesis that energy partitioning is under genetic control (Veerkamp et al., 2003). The greater BCS, lower BCS loss across lactation, and lower milk yield reported with the MB and NM relative to that of the HF in the present study are similar to the findings of Dillon et al. (2003a).

Body condition score has been shown to be favorably correlated with reproductive performance, both phenotypically (Buckley et al., 2003) and genetically (Berry et al., 2003a). In a seasonal system in which grazed grass constitutes a large proportion of the diet, such

Figure 3. Survival curves for the Holstein-Friesian (●), Montbéliarde (■), Normande (▲), Norwegian Red (○), Montbéliarde × Holstein-Friesian (□), and Normande × Holstein-Friesian (▲) across days postcalving.

as in Ireland, Buckley et al. (2003) reported reduced 21-d submission rate, PREG1, and PREG42 for HF in low BCS. Lower SR24 and FINALPR were reported here for the HF compared with other breeds. The performance of the NRF is consistent with the breeding objectives for the breed. Female fertility has been included in the Norwegian total merit index since 1972, the relative weighting of which increased from 5% in 1974 to 14% in 1997 (Andersen-Ranberg et al., 1998). A genetic analysis of the French dairy cattle population showed a decline in the reproductive performance of the Holstein breed in the past decade, whereas repro-

ductive performance of the MB and NM have remained stable over the same period (Boichard et al., 2002). Previous research reported that varying levels of concentrate offered in tandem with adequate amounts of high-quality pasture resulted in no improvement in reproductive performance (Snijders et al., 2000; Horan et al., 2005b). Greater BCS and BW throughout lactation were observed in animals on the HC diet; however, differences between the feeding systems were small.

Results from the current study contrast with those of Dillon et al. (2003b), who reported greater conception rate to first service and submission rate in the first 3

Table 4. Least squares means for breed of dairy cow¹ for plasma metabolites around parturition and mating start date (MSD)

Variable	Breed ²						SEM ⁴	P-value ³		
	HF	MB	NM	NRF	MBX	NMX		B	T	B × T
Log _e insulin										
Precalving	1.13 (3.11)	0.88 (2.40)	1.22 (3.39)	1.32 (3.74)	1.31 (3.72)	1.33 (3.76)	0.181	NS	<0.001	NS
Calving	0.77 (2.16)	0.78 (2.17)	1.06 (2.90)	0.91 (2.49)	0.79 (2.20)	0.86 (2.35)	0.165			
Postcalving	1.04 (2.83)	0.82 (2.27)	1.01 (2.73)	0.74 (2.09)	0.92 (2.51)	1.07 (2.91)	0.172			
MSD	1.27 (3.54)	1.29 (3.62)	1.22 (3.38)	1.11 (3.03)	1.31 (3.70)	1.31 (3.70)	0.213			
IGF-1 (ng/mL)										
Precalving	126.3	124.3	116.6	139.6	107.1	122.7	10.56	NS	<0.001	NS
Calving	55.1	72.3	76.5	69.5	61.9	54.6	10.34			
Postcalving	91.6	94.8	106.0	96.2	82.8	79.6	11.00			
MSD	89.8	120.6	117.7	100.8	108.0	97.9	11.34			

¹HF = Holstein-Friesian; MB = Montbéliarde; NM = Normande; NRF = Norwegian Red; MBX = Montbéliarde × Holstein-Friesian; NMX = Normande × Holstein-Friesian.

²Back-transformed insulin least squares means are presented in parentheses.

³B = breed effect; T = effect of time period; B × T = effect of interaction between breed and time period.

⁴SEM is the pooled SEM.

wk of the breeding season for the MB compared with the HF. Our results showed that SR24 and PREG1 did not differ between the HF and MB, which was reflected in the similarity of PREG42 between the breeds. However, the probability of FINALPR was greater in the MB compared with the HF, indicating that a greater proportion of MB conceived late in the breeding season. This factor, coupled with the longer gestation length of the MB (Dillon et al., 2003b), contributed to the later calving day of year for the MB breed, the effect of which was cumulative as parity increased. Collectively, the results indicate that, relative to the other breeds, the lower survival of the MB was partly due to an inability to maintain a 365-d calving interval, whereas that of the HF was largely due to their reduced ability to conceive during the breeding season. Differences in CTFS between the breeds, although statistically different, are not deemed to be of practical significance (i.e., are not expected to have influenced differences in reproductive performance across the breed groups).

Heins et al. (2006b) evaluated the reproductive efficiency of HF, NMX, MBX, and Scandinavian Red $\times$ HF during first lactation. Their results showed that the crossbreds had fewer days to first breeding, had greater first-service conception rates, had fewer days open, and survived longer compared with the purebred HF during first lactation. The present study also found that both crossbred groups were more likely to be pregnant at the end of the breeding season and had greater survival rates compared with the HF; however, heterosis estimates for these traits were not significant, which is likely due to the small size of the data set. Lopez-Villalobos et al. (2000) reported advantages of crossbreeding under New Zealand's seasonal-calving pasture-based system of production through a reduction in replacement rates and greater milk, fat, and protein yields, which were attributable to the ability of the crossbreds to survive longer in the herd. In Ireland, the potential to improve profitability and reproductive efficiency by crossbreeding is generating interest.

Negative energy balance in the early postpartum period has been cited as the critical regulator of reproductive status, as defined by the animal's ability to resume cyclicity (Butler and Smith, 1989). Early reestablishment of luteal activity postpartum has been suggested as an indicator trait to select for improved fertility (Darwash et al., 1997; Royal et al., 2000; van der Lende et al., 2004). In nonseasonal dairy systems, Royal et al. (2000) reported lower conception rates for animals with short (≤ 12.9 d) or long (≥ 49 d) CLA. Darwash et al. (1997) reported greater conception rates in animals that ovulated earlier postpartum. However, McNaughton et al. (2007) concluded that in a seasonal grass-based dairy system, CLA was not related

to fertility; however, prolonged CLA postpartum (>70 d) reduced submission rate by decreasing the proportion of animals available for service at the start of the breeding season. Therefore, it will be necessary to take into account different dairy production systems when considering fertility traits for genetic improvement. Royal et al. (2000) reported a significant increase in LP length of nearly 2 d from 1975 to 1998, which coincided with the upgrade in the national herd from British-Friesian to HF. Our results showed that the HF and NRF had the greatest difference in the first and average LP length; however, this was not statistically different. Royal et al. (2000) suggested that the length of the LP might provide an indication of uterine environment. Although no analysis was undertaken to determine associations between reproductive performance and luteal traits, differences between the breeds in fertility may relate to some underlying difference in endometrial or uterine environment.

Negative energy balance reduces plasma insulin and IGF-1 concentrations in early lactation. This can lead to poorer ovarian follicular development, thus compromising reproductive efficiency (Butler, 2003). Plasma IGF-1 concentrations decrease after calving and rise gradually as energy status of the cow improves (McGuire et al., 1992). Results from the current study showed that insulin and IGF-1 profiles followed this natural trend. However, breed did not influence insulin and IGF-1 profiles in the periparturient period. In a study comparing Jersey, Friesian, and crossbred cows on an all-pasture system, Back et al. (2006) reported no difference between the breeds in IGF-1 concentrations in the first 6 wk of lactation. Low IGF-1 concentrations have been associated with a delay in CLA (Roberts et al., 1997). Our results and those of Back et al. (2006) revealed no difference between the breeds in CLA. Similarly, no difference in CLA and IGF-1 concentrations were observed in different strains of HF in early lactation (Horan et al., 2005b; McCarthy et al., 2007).

In Ireland, as in many other countries worldwide, the HF is by far the most popular dairy cow breed (Irish Cattle Breeding Federation, 2006). However, potential improvements in overall profitability, largely driven by improved fertility and health potentially gained from crossbreeding, is generating interest among dairy farmers. Taking the results of the current study and the results of the previous study from the same experiment (Walsh et al., 2007) collectively, it would appear that of the 3 alternative breeds evaluated, the NRF is more suited to a seasonal grass-based system of milk production. Although the NRF produced slightly less milk compared with the HF, the breed displayed many favorable traits, namely, superior reproductive efficiency, superior udder health, and a moderate size.

Therefore, crossbreeding with the NRF may lead to improved profitability in many dairy herds. However, despite the positive indications, the scale and depth of the current study must be taken into account. Further research with larger numbers is warranted before conclusive recommendations pertaining to the NRF breed or crossbreed can be made. Robust estimates of the relative breed and heterosis effects are paramount. As elsewhere, inbreeding levels in dairy and beef breeds in Ireland are increasing (Mc Parland et al., 2007). Thus, crossbreeding to avoid the negative impact of inbreeding depression is a viable option.

CONCLUSIONS

This study confirmed differences in milk production potential between the breeds. The HF, selected for greater milk production, had lower BCS and greater BW throughout lactation compared with the NRF, selected for functional traits concurrently with milk production. The MB and NM, selected simultaneously for milk and beef production, had greater BCS compared with all breeds over the complete lactation. Some differences between the breeds in their capacity to establish and maintain pregnancy were observed despite similarities in their endocrine and metabolic hormone profiles. The HF was less likely to be pregnant at the end of the breeding season; thus, their ability to survive in a seasonal production system may be compromised. Feeding system did not influence reproductive performance of the different breeds.

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