The influence of genetic selection and feed system on the reproductive performance of spring-calving dairy cows within future pasture-based production systems

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ABSTRACT

Three genetic groups of Holstein-Friesian dairy cows were established from within the Moorepark (Teagasc, Ireland) dairy research herd: LowNA, indicative of the Irish national average-genetic-merit North American Holstein-Friesian; HighNA, high-genetic-merit North American Holstein-Friesian; HighNZ, high-genetic-merit New Zealand Holstein-Friesian. Genetic merit in this study was based on the Irish total merit index, the Economic Breeding Index. Animals from within each genetic group were randomly allocated to 1 of 2 possible post-European Union-milk-quota pasture-based feeding systems (FS): 1) The Moorepark (MP) pasture system (2.64 cows/ha and 500 kg of concentrate supplement per cow per lactation) and 2) a high output per hectare (HC) pasture system (2.85 cows/ha and 1,200 kg of concentrate supplement per cow per lactation). A total of 126, 128, and 140 spring-calving dairy cows were used during the years 2006, 2007, and 2008, respectively. Each group had an individual farmlet of 17 paddocks, and all groups were managed similarly throughout the study. The effects of genetic group, FS, and the interaction between genetic group and FS on reproductive performance, body weight, body condition score, and blood metabolite concentrations were studied using mixed models with factorial arrangements of genetic groups and FS. Odds ratios were used in the analysis of binary fertility traits, and survival analysis was used in the analysis of survival after first calving. When treatment means were compared, the HighNA and HighNZ genotypes (with greater genetic merit for fertility performance) had greater first-service pregnancy rates and had a greater proportion of cows pregnant after 42 d of the breeding season than the LowNA group. Both HighNA and HighNZ genotypes were submitted for artificial insemination earlier in the breeding season and had greater survival than the LowNA genotype. There

was no significant FS or genotype by FS interactions for any of the reproductive, blood metabolite, body weight, or body condition score measures. The results demonstrate that increased genetic merit for fertility traits resulted in improved reproductive performance and that the poor reproductive capacity of inferior-genetic-merit animals for fertility was not improved through concentrate supplementation at pasture.

Key words: Holstein-Friesian dairy cow, genotype, feed system, reproductive performance

INTRODUCTION

Reproductive performance has declined in modern dairy production systems concurrent with aggressive selection for milk production (Pryce et al., 1997). It is now widely accepted that within pasture-based milk production systems, which account for approximately 10% of global milk production, potential gains in herd production are not being realized because of reproductive wastage (Evans et al., 2006). Such systems are typically based on achieving synchrony between calving patterns, feed demand, and pasture growth to maximize pasture utilization. Unlike confinement systems, reproductive wastage within pasture-based systems results in additional financial losses due to a reduction in pasture utilization and lower milk productivity arising from extended calving intervals and a shortening of lactation length. Within Irish milk production systems, Evans et al. (2006) observed a reduction in calving rate to first insemination of approximately 1% per year from 55% in 1990 to 44% in 2001. Royal et al. (2000) found similarly declining reproductive performance in the United Kingdom between 1975 and 1995. The low levels of reproductive efficiency within Irish pasture-based production systems are corroborated by Irish national dairy herd fertility statistics where the current annual calving interval is 396 d and on average only 57% of cows calve within the first 42 d of the calving season (ICBF, 2008).

Traditionally, genetic selection programs have predominantly focused on milk production but recently

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have been expanded to include more functional traits such as durability, health, and reproduction (Miglior et al., 2005). The Economic Breeding Index (**EBI**), launched in Ireland in 2001, is a dairy cattle breeding objective, derived under Irish conditions, to identify genetically superior animals for profitability (Berry et al., 2007). Traits included in the EBI (relative emphasis in parentheses) are milk production (42%), fertility (37%), beef performance (9%), calving performance (8%), and health (5%) (Berry et al., 2007).

Numerous studies have associated inferior reproductive performance with the partitioning of nutrients in the body, which is reflected by differences in various blood metabolites such as glucose, NEFA, BHBA, albumin, urea, protein, and hormones such as insulin and IGF-1 (Butler 1998; Clark et al., 2005; Hammon et al., 2005). Animals selected for higher milk production have exhibited higher blood NEFA and BHBA but lower concentrations of glucose (Clark et al., 2005). Similarly, elevated plasma urea nitrogen concentrations are associated with increased ammonia and urea nitrogen concentrations and can result in inferior fertility performance (Hammon et al., 2005). Prolonged and more severe periods of negative energy balance (**NEB**) result in the draining of body reserves from the animal causing increased amounts of BW and body condition losses. Increased losses of body condition have been shown to negatively affect fertility (Butler and Smith, 1989; Buckley et al., 2003). Horan et al. (2005) showed that significant differences exist between strains of Holstein-Friesian (**HF**) in BCS profiles across lactation and highlighted the potential to influence BCS profiles through feed management; however, Kolver et al. (2005) showed that although concentrate supplementation to increase total feed intake can increase BCS, differences in BCS due to nutritional management within a strain or breed have no effect on reproductive performance.

Recent analysis carried out within the European Union (**EU**) suggests that milk quotas are now constraining the development of an efficient European dairy industry (van Berkum and Helming, 2006). Currently, Irish dairy farm systems are characterized by stocking rates of 1.9 cows/ha and average per cow concentrate supplementation of 700 kg (National Farm Survey, 2007). Lips and Rieder (2005) projected that milk quota abolition would allow production to move to areas of competitive advantage within Europe such as Denmark, Ireland, and the Netherlands, predicting that milk production in Ireland could increase by up to 39% after the abolition of milk quotas. Following impending EU Common Agricultural Policy (CAP) reforms resulting in the abolition of milk quotas, milk production systems will change rapidly, resulting in more volatile milk prices and consequently a requirement for increased

technical efficiency to maintain farm incomes. Milk quota removal will necessitate innovation, productivity gain, and increased operational scale at the farm level as the dairy industry evolves, through intensification of production systems in terms of stocking rates and a greater reliance on a predominantly grass-based diet (Dillon et al., 2008). Similar agricultural reforms have occurred in many other countries and have stimulated a dramatic change in production system characteristics with increased herd sizes (Davison, 1995), reductions in supplementary input usage (Blandford and Dewbre, 1994), and increased stocking densities as systems adapt to increase overall production efficiency (Philpott, 1995).

Research evaluating genetic influences on reproductive performance has traditionally compared animals of high, medium, or low merit for productive traits without cognizance of prevailing industry standards (Buckley et al., 2000). Previous studies have compared diverse strains of dairy cattle and reported large variability in reproductive performance both within Ireland (Horan et al., 2004) and internationally (Harris and Kolver, 2001). These studies have rarely compared strains of equal overall genetic merit within a breed. Similarly, research evaluating genetic influences on system characteristics such as stocking rate or levels of concentrate supplementation have generally focused on the individual system components (Buckley et al., 2000; Horan et al., 2004) rather than the likely combination of both within an overall farming system. The objective of this study, therefore, was to quantify the effect of genetic improvement using the Irish total merit index, the EBI, on the reproductive performance of the Irish dairy herd within likely intensive pasture-based production systems post-EU milk quota and the effect of improving energy status through increased feed intake on observed performance.

MATERIALS AND METHODS

This study was carried out at Moorepark dairy research center in Ireland (55°10' N, 8°16' W) over a 3-yr period (2006, 2007, and 2008). A total of 391 lactations from 219 spring-calving HF dairy cows were used as part of the trial, with 126, 128, and 140 cows in yr 1, 2, and 3, respectively (Table 1). Cows were assigned to genetic group based on genetic merit (measured as pedigree index for EBI) and origin [North America (**NA**) or New Zealand (**NZ**)]. These animals were then randomly allocated to 1 of 2 pasture-based feeding systems (**FS**) in a 3 × 2 factorial arrangement (3 genetic groups × 2 FS). The current analysis formed part of a larger overall study designed to examine the biological

Table 1. Number of cows and lactation records within each genotype and feed system for each year of the study

Item	Genotype ¹			Feed system ²	
	LowNA	HighNA	HighNZ	MP	HC
Animals (n)					
Year 1	42	42	42	63	63
Year 2	42	42	44	64	64
Year 3	46	46	48	70	70
Lactation records (n)					
Parity 1	40	40	43	62	61
Parity 2	35	28	32	50	45
Parity 3 +	59	63	58	87	93

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Feed systems: MP = Moorepark; HC = high output per hectare.

and economic effect of genetic improvement across 2 likely intensive post-EU-milk-quota pasture-based FS.

Animals

Three genetic groups of HF dairy cattle were established for this study from within the Moorepark dairy research herd based on their origin and overall genetic merit as measured by pedigree index for EBI. The genetic groups compared were 1) average-genetic-merit dairy cow of North American HF origin indicative of the current Irish national herd (**LowNA**); 2) high-genetic-merit North American HF (**HighNA**); and 3) high-genetic-merit New Zealand HF (**HighNZ**). The mean pedigree index (of each individual cow calculated

from the total merit index of the sire and maternal grandsire obtained from the autumn 2008 International Bull Evaluation Service, Uppsala, Sweden) for each genetic group for milk production and fertility traits is summarized in Table 2.

To generate the LowNA genetic group, a subsample of cows, ranked on EBI representing the characteristics of the national average genetic merit dairy cow on Irish dairy farms at the time of the study (Irish Cattle Breeding Statistics, 2006–2008; ICBF, 2008) was created from within the Moorepark herd representing progeny of 12 sires of North American ancestry. These animals were used to quantify the reproductive capacity of the Irish dairy herd within intensive futuristic production systems in the absence of the EBI as a

Table 2. The mean Economic Breeding Index (EBI) and EBI sub-indices¹ for the 3 genotypes of Holstein-Friesian cows studied averaged across lactation records (n = 391) based on their PTA for milk production, calving interval, and survival

Item	Genotype ²			SD ³
	LowNA	HighNA	HighNZ	
EBI	48.8 ^a	74.6 ^b	87.8 ^c	26.66
Sub-indices				
Milk (€)	41.9 ^a	40.0 ^a	47.8 ^b	11.68
Fertility (€)	5.3 ^a	25.7 ^b	41.7 ^c	23.79
Calving (€)	8.5 ^a	13.6 ^b	17.2 ^c	3.65
Health (€)	−4.5 ^a	−3.7 ^b	−14.2 ^c	3.02
Beef (€)	−2.4 ^a	−1.0 ^a	−4.7 ^b	6.27
PTA				
Milk (kg)	133.7 ^a	117.0 ^a	92.2 ^b	72.82
Fat (%)	0.02 ^a	0.04 ^b	0.11 ^c	0.067
Protein (%)	0.04 ^a	0.04 ^a	0.07 ^b	0.029
Calving interval (d)	−0.21 ^a	−1.44 ^b	−2.41 ^c	1.43
Survival (%)	0.25 ^a	0.76 ^b	1.15 ^c	0.76

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

¹Obtained from the 2008 sire and maternal grandsire international evaluations of the Interbull Centre (Uppsala, Sweden) using the multiple across-country evaluation technique.

²Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

³SD = pooled standard deviation.

method for genetic improvement of fertility traits. The HighNA genetic group was generated as a subsample of the highest 25% of animals on EBI of North American ancestry from within the Moorepark herd representing progeny of 14 sires of North American ancestry. The HighNA group was established to represent the effect of genetic improvement using high-EBI North American HF sires incorporating improved fertility performance. Replacement animals were generated using the top sires on EBI of North American HF ancestry each year. The HighNZ animals were the progeny of embryos imported in 1998 from New Zealand and implanted into 13-mo-old heifers at Moorepark. These embryos were generated by mating high-genetic-merit New Zealand HF cows (expressed in the New Zealand genetic evaluation system, Breeding Worth) with high-genetic-merit New Zealand HF sires. The resulting herd has been perpetuated by mating the New Zealand females to sires of New Zealand origin, representing progeny of 13 sires. This group was established to compare the effects of genetic improvement through high-EBI New Zealand HF ancestry compared with North American HF ancestry of equally high overall genetic merit. The HighNZ herd represents a HF that was selected within a seasonal pasture-based system in New Zealand that is similar to Irish pasture-based systems but with greater emphasis on compact seasonal-calving fertility targets. The average percentage North American Holstein genes in the LowNA and HighNA animals was 90% compared 12.5% for HighNZ animals.

Feeding Systems

During the dry period all animals were managed similarly on an *ad libitum* grass silage diet. Animals were randomly allocated to 1 of 2 possible post-EU-milk-quota pasture-based FS: 1) the Moorepark (MP) pasture system; a high grass allowance, high stocking rate, and low concentrate input system (2.64 cows per ha and a concentrate input of 500 kg per cow per lactation) and 2) a high output per hectare (HC) system, higher stocking rate FS (2.85 cows per ha and a greater concentrate input of 1,200 kg per cow per lactation). The MP FS was designed as a pasture management system for a post-EU-milk-quota scenario based on high levels of pasture utilization and a low level of concentrate supplementation. The HC FS was created as a high-productivity pasture system to increase milk output per hectare by supplementing pasture with concentrates and increasing stocking rate to ensure similar high levels of pasture utilization. In HC FS, grass intake per cow was reduced and replaced in the diet with concentrates. All multiparous cows remained on the same FS for the duration of the study and were assigned

to FS immediately postpartum. All primiparous cows were managed similarly for the first 4 wk of lactation to derive pre-experimental milk production performance, which was then used to allocate animals within genetic group to FS.

A total of 50.08 ha of permanent grassland containing greater than 80% perennial ryegrass (*Lolium perenne*) was used for the duration of the study. A separate farmlet of 17 paddocks was created for each of the 6 treatment groups, and each farmlet was balanced for location and soil type. All groups were managed similarly on a common rotation length and grazed to a similar intensity based on postgrazing residual sward surface height throughout the lactation. All groups grazed similar pregrazing herbage masses of 1,200 kg of DM/ha (>4 cm) and grazed to an average postgrazing residual height of 4.73 cm. To account for the stocking rate differential, paddock size for the HC FS was 8% smaller than for the MP FS, and a differential of 3 kg of concentrate was maintained between the MP and HC FS throughout the grazing season. Table 3 shows the effect of FS on concentrate supplementation and daily feed allowances during the experiment. Concentrate supplementation for the MP FS commenced at 4 kg per cow per day postcalving and was reduced and removed once grass supply allowed, usually in mid-March. Concentrates were only reintroduced to the MP FS during the remainder of the season if grass supply was reduced to below target levels. In 2006, because of a mid-summer drought, concentrate was reintroduced at a rate of 4 kg per cow per day for the MP FS and increased to 8 kg/d for the HC FS for 52 d from June to September; in November 2008, concentrate was reintroduced for 18 d at a rate of 3 kg per cow per day for the MP FS and increased to 6 kg/d for the HC FS because of inclement weather and poor pasture growth. Concentrates were supplied twice daily (during morning and evening milking) through the parlor. The ingredient composition of the concentrate feed was as follows: barley 25%, corn gluten 26%, beet pulp 35%, soybean meal 11%, and minerals plus vitamins 3%.

Reproductive Management

At approximately 35 to 42 d postpartum each cow was examined using transrectal ultrasound imaging (Aloka SDD 500V scanner with a 5-MHz transducer, Aloka Ltd., Tokyo, Japan) to detect ovarian or uterine disorders and to ensure the cows had re-established ovarian activity. Cows with reproductive disorders (such as endometritis, pyometra, or ovarian cysts) were recorded and treated as necessary using standard veterinary procedures. For the duration of the breeding season, cows were observed for estrus a minimum of 4 times daily

Table 3. The effects of feed system on concentrate supplementation and daily feed intake (kg of DM/cow) during the experiment

Item	Feed system ¹		SE ²	P-value
	MP	HC		
Cumulative concentrate supplementation (kg of DM/cow)				
Total lactation	383	1,245	9.7	<0.001
To mating start date	183	283	8.7	<0.001
To mating finish date	221	611	8.9	<0.001
Daily feed allowance during the AI season (kg of DM/cow)				
Herbage allowance	16.2	14.5	0.06	<0.001
Concentrate intake	0.4	3.4	0.02	<0.001
Total allowance	16.6	17.9	0.06	<0.001

¹Feed systems: MP = Moorepark; HC = high output per hectare.

²SE = pooled standard error.

(0630, 1200, 1500, and 2000 h). Tail paint was used as a heat detection aid and was reapplied when necessary. Cows were inseminated following signs of heat using AI over a 13-wk breeding season that commenced in mid to late April each year. During the breeding season, all cows showing signs of heat were inseminated regardless of calving date. The same professional inseminator performed AI for each year of the study. Cows detected on heat before morning milking (0630 h) were inseminated that morning, whereas cows detected subsequently that day were inseminated the following morning. All cows were inseminated with thawed-frozen semen from sires of their own genetic group to generate replacement heifers. Semen quality was verified for all sires selected for use during the breeding season before being used in the experiment. Ultrasonographic examination was conducted at approximately 30 to 37 and 60 to 67 d post-AI and at 150 d after the beginning of the breeding season to determine pregnancy status and overall pregnancy rates.

BW, BCS, and Reproductive Measurements

Individual animal BW was recorded weekly upon exit from the milking parlor using an electronic scale (Tru-Test Ltd., Auckland, New Zealand) calibrated weekly against known weights. Animal BCS was assessed every 3 wk throughout the study on a 1 to 5 scale (1 = thin, 5 = fat) in increments of 0.25 as outlined by Edmonson et al. (1989). Body condition was assigned by one individual throughout the study. The following reproductive measurements were calculated and analyzed: mean calving date, 24-d submission rate (calculated based on an animal being served within the first 24 d of the breeding season irrespective of calving date), calving to first service interval (interval in days from calving to first service), calving to conception interval (interval in days from calving to conception), services per cow

(number of inseminations per cow during the breeding season), conception rate to first service, pregnancy rate after the first 42 d of the breeding season, embryonic mortality, overall pregnancy rate (confirmed by rectal palpation 150 d after the start of breeding season), and survival (number of days from date of first calving on trial to date of culling or end of trial).

Blood Measurements

Blood samples were taken from all cows approximately 4 times throughout the season: 28 to 35 d precalving, 0 to 7 d postcalving, and 28 to 35 d postcalving for all 3 yr, and at the start of the breeding season for yr 2 and 3. All blood samples were taken in accordance with the guidelines set by Ireland's Cruelty to Animals Act of 1876. Blood was sampled by coccygeal venipuncture after morning milking and centrifuged within 2 h of collection for 15 min at 5°C and 1,470 × *g*. The plasma was then split into borosilicate glass scintillation vials and stored at –20°C until analysis (McCarthy et al., 2007a). The metabolites and hormones analyzed were glucose, NEFA, BHBA, urea, protein, albumin, and insulin. Glucose, NEFA, BHBA, urea, protein, and albumin concentrations were quantified by enzymatic calorimetry using ABX Mira Auto analyzer (ABX Mira, Montpellier, Cedex 4, France). Plasma insulin concentrations were quantified using fluoro-immunoassay (AutoDELFIA, PerkinElmer Life and Analytical Sciences, Turku, Finland). Inter- and intraassay coefficients of variation were 5.36 and 5.50%, respectively.

Statistical Analysis

Dietary Details. Feed system differences in total annual concentrate supplementation, supplementation total to mating start date, supplementation total to the end of breeding, daily herbage allowance, and daily

concentrate intake were determined using mixed models (Proc Mixed, SAS Institute, 2006) with cow included as a repeated effect; a first-order autoregressive covariance structure with heterogeneous variances provided the best fit for the data. The effects of genotype, year, FS, and their interactions were tested as fixed effects; however, only year and FS were included in the final model.

BW, BCS, and Fertility Performance. The effects of genotype and FS on BW, BCS, calving date, calving to first-service interval, calving to conception interval, and calving interval was determined using mixed models (Proc Mixed, SAS Institute, 2006) with cow included as a repeated effect; a compound symmetry covariance structure among records within cow provided the best fit to the data. The effects of year, parity, calving date, genotype, FS, and their interactions were tested, with only significant effects ($P < 0.05$) remaining in the final models. Number of services per cow was analyzed using the Kruskal-Wallis non-parametric test (PROC NPAR1WAY, SAS Institute, 2006). Binary data (pregnancy rate to first and second service, 42-d pregnancy rate, submission rate, embryo mortality, and overall pregnancy rates) were analyzed using generalized estimated equations (GEE; Proc Genmod, SAS Institute, 2006); a logit link function was used and a binomial distribution was assumed. The effects of genotype, FS, year, parity, and calving date were tested with only significant effects remaining in the final models. Significance was declared at $P < 0.05$ based on the GEE score statistic. Odds ratios were calculated as the exponent of the model solutions. The odds ratio is an estimation of the relative odds of an event (e.g., likelihood of a positive outcome) occurring in the exposed group relative to a reference group or class. In all cases, the LowNA genetic group and the HC FS were used as the reference groups. Therefore, an odds ratio of 1 represents an equal likelihood of an event occurring to an animal in a particular group compared with a contemporary in the reference group. An odds ratio greater than 1 indicates a greater likelihood of that particular event occurring relative to the reference group.

The effect of genotype and FS on survival was performed using survival analysis (Proc TPHREG, SAS Institute, 2006); data included 219 animals. Date and reason for removal from the study were recorded for all animals. A total of 113 animals were pregnant and still present on the farm at the end of the study. These animals were assumed censored on the last day of the year 2008. Animals removed from the study as surplus were also coded as right-censored on the date of exit from the farm. All other animals were treated as culled on the respective date of culling. Genotype and FS were

included as fixed effects in the model. Survival was expressed as the relative hazard of a cow being culled at day t , given that it had not been culled at day $t - 1$ in the exposed group relative to the reference group. The LowNA genetic group and the HC FS were used as the reference groups. Therefore, a hazard ratio of 1 represents an equal likelihood of a cow being culled compared with a contemporary in the reference group. A lower hazard ratio indicates a decreased likelihood of an animal being culled compared with the reference group.

Blood Metabolites and Hormones. The natural logarithm transformation of insulin, NEFA, and BHBA levels was used to normalize the distributions. Two separate types of analyses were undertaken. The blood samples taken at precalving, calving, and postcalving were analyzed together with a separate analysis for samples taken at the start of the breeding season. The effects of stage (i.e., precalving, calving, and postcalving) and genotype on blood metabolites and hormones were determined using mixed models (SAS Institute, 2006). Cow was included as a repeated effect with a compound symmetry covariance structure with heterogeneous variances fitted among records within animals. Initial models included the effects for genotype, parity, stage, FS, calving date, year, and their interactions. Nonsignificant effects ($P > 0.05$) were removed from the model. Additionally, the effects of genotype and FS were determined on the sample taken at mating start date in yr 2 and yr 3 using mixed models (SAS Institute, 2006). Cow was included as a repeated effect; a compound symmetry covariance structure with heterogeneous variances provided the best fit for the data. Initial models included the effects for genotype, parity, stage, FS, calving date, year, and interactions. Nonsignificant effects ($P > 0.05$) were removed from the model.

RESULTS

Reproduction and Fertility Performance

There was no interaction between genotype and FS observed for any of the reproductive variables investigated; therefore, only main effects are reported (Table 4). Calving dates ranged from January 12 to April 30, January 13 to April 18, and January 19 to May 10 in yr 1, 2, and 3 of the study, respectively. Although all groups commenced the study with a similar mean calving date, the LowNA group had a later mean calving date over the latter 2 yr of the study compared with both other genotypes. There was no significant difference in number of days from calving to service interval, calving to conception interval, calving interval, or ser-

Table 4. Effect of genotype of Holstein-Friesian and feed system on reproduction and fertility performance

Item	Genotype ¹					Feed system ²			
	LowNA	HighNA	HighNZ	SE ³	P-value	MP	HC	SE ³	P-value
Mean calving date (date)	Feb 28 ^a	Feb 22 ^{ab}	Feb 18 ^b	2.1	0.004	Feb 24	Feb 22	1.7	0.47
Calving to service interval (d)	73.2	72.6	78.4	2.13	0.10	73.6	75.9	1.71	0.33
Calving to conception interval (d)	103.2	104.8	104.8	2.91	0.90	104.1	104.5	2.39	0.89
Calving interval (d)	384.9	384.1	382.1	2.69	0.75	382.2	385.1	2.28	0.38
Services per cow (n)	2.09	1.89	1.83		0.14	1.91	1.96		0.63

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

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Feed systems: MP = Moorepark; HC = high output per hectare.

³SE = pooled standard error.

vices per cow between genotypes. Feed system had no effect on any of the reproductive variables measured.

The effect of genotype of HF and FS on the binary fertility variables and survival are displayed in Table 5. There were no interactions between genotype and FS, so only the main effects are described. Feed system had no effect on either the fertility performance variables or survival. Both HighNA and HighNZ animals had increased odds of being submitted for AI, being pregnant to first insemination, and being pregnant after 42 d of the breeding season compared with LowNA animals. Submission rates were significantly greater ($P < 0.05$) for HighNA and HighNZ (93.0 and 90.3%, respectively) compared with LowNA (72.7%). Pregnancy rate to first insemination and pregnancy rate after 42 d of the breeding season were greatest for HighNZ animals (56.7 and 67.9%, respectively), lowest for LowNA animals (35.9 and 50.4%, respectively), and intermediate for HighNA (45.2 and 61.1%, respectively). There were no differences observed in embryo mortality or overall pregnancy rate between genotypes during the study. Embryo mortality and overall pregnancy rate were not different between genotypes, averaging 11.4 and 79.9%, respectively. The

HighNA and HighNZ had significantly lower hazard of being culled compared with the LowNA group.

BW and BCS

Because there were no interactions between genotype and FS for BW or BCS characteristics from calving to the end of the breeding season, only the main effects are detailed in Table 6. Body weight was similar for both NA genotypes compared with the lighter weight HighNZ genotype at calving and the end of the breeding season. All genotypes were lighter at mating start date compared with at calving and were heavier at the end of the breeding season compared with BW at mating start date; however, HighNZ lost the least amount of BW postcalving and gained the least BW during the breeding season compared with both NA genotypes. There was no difference in BW between the 2 FS at any of the measurement points from calving up to the end of the breeding season; however, animals on the MP FS lost more BW compared with animals on the HC FS from calving to the start of the breeding season.

Table 5. Effect of genotype of Holstein-Friesian and feed system on odds and hazard ratios for fertility performance variables (95% confidence intervals are included in parentheses)

Item	Genotype ¹			Feed system ²	
	HighNA	HighNZ	P-value	MP	P-value
24-d submission rate ³	5.77 (2.47, 13.51)	3.66 (1.75, 7.62)	<0.001	0.81 (0.46, 1.47)	0.51
Pregnancy rate to first service ³	1.59 (0.91, 2.80)	2.38 (1.37, 4.11)	0.008	0.87 (0.55, 1.37)	0.55
42-d pregnancy rate ³	1.69 (0.98, 2.88)	2.19 (1.22, 3.91)	0.03	1.11 (0.71, 1.74)	0.64
Embryo mortality ³	1.04 (0.50, 2.18)	0.65 (0.27, 1.50)	0.45	1.40 (0.72, 2.71)	0.31
Overall pregnancy rate ³	1.42 (0.77, 2.60)	1.73 (0.91, 3.29)	0.22	0.96 (0.57, 1.62)	0.88
Survival ⁴	0.68 (0.47, 0.98)	0.43 (0.29, 0.65)	<0.001	0.80 (0.59, 1.10)	0.18

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Feed systems: MP = Moorepark; HC = high output per hectare.

³Expressed as odds ratios and 95% confidence intervals; LowNA and HC used as reference categories.

⁴Expressed as hazard ratios and 95% confidence intervals; LowNA and HC used as reference categories.

Table 6. Effect of genotype of Holstein-Friesian and feed system on BW and BCS profiles from calving to the end of the breeding season

Item	Genotype ¹					Feed system ²			
	LowNA	HighNA	HighNZ	SE ³	P-value	MP	HC	SE ³	P-value
Calving BW	630 ^a	647 ^a	605 ^b	8.1	<0.001	630	624	6.9	0.47
BW at mating start date	550 ^{ab}	560 ^a	537 ^b	5.5	0.003	546	552	4.5	0.14
BW at end of breeding season	581 ^a	591 ^a	557 ^{ab}	5.1	<0.001	575	578	3.9	0.37
BW change from calving to breeding	80.7 ^a	85.7 ^a	66.8 ^b	5.54	0.01	84.1	71.4	4.81	0.02
BW change during breeding season	30.0 ^a	31.3 ^a	17.7 ^b	2.77	<0.001	27.7	24.9	2.43	0.29
Calving BCS	3.02 ^a	3.14 ^b	3.16 ^b	0.027	<0.001	3.09	3.11	0.023	0.38
BCS at mating start date	2.74 ^a	2.82 ^b	2.92 ^c	0.030	<0.001	2.78	2.87	0.026	<0.001
BCS at end of breeding season	2.78 ^a	2.83 ^a	2.94 ^b	0.024	<0.001	2.81	2.89	0.018	<0.001
BCS change from calving to breeding	0.28 ^{ab}	0.32 ^a	0.22 ^b	0.026	0.02	0.31	0.24	0.023	0.003
BCS change during breeding season	0.04	0.01	0.02	0.022	0.68	0.03	0.02	0.019	0.91

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

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Feed systems: MP = Moorepark; HC = high output per hectare.

³SE = pooled standard error.

Body condition score at calving was lower for LowNA compared with both HighNA and HighNZ genotypes; however, HighNA had the greatest loss in body condition between calving and mating start date, whereas HighNZ had the least. At mating start date, LowNA had the lowest BCS and HighNA was intermediate, whereas HighNZ had the greatest BCS at mating start date and at the end of the breeding season with changes in BCS during the breeding season not different between genotypes. Although animals on both FS had similar BCS at calving, animals on the HC FS had a greater BCS at mating start date and at the end of the breeding season because of reduced loss in body condition between calving and mating start date compared with animals on the MP FS. There was no difference in BCS change between mating start date and the end of the breeding season between the 2 FS.

Blood Metabolite and Hormone Concentrations

The effect of genotype of HF on blood metabolite and hormone concentrations around parturition is displayed in Table 7. Precalving, both FS were fed ad libitum grass silage without concentrate supplementation and both FS were allocated concentrates for the first 4 wk postpartum before MP FS went on a grass-only diet. Therefore, there was no FS effect. Only NEFA concentrations were affected by genotype ($P < 0.05$), with greatest concentrations observed in HighNZ animals (0.19 mmol/L), whereas HighNA animals were lowest (0.16 mmol/L) and LowNA animals were intermediate (0.18 mmol/L). Stage of blood sampling around parturition affected ($P < 0.001$) all blood metabolites and hormones measured. Insulin concentrations were greatest precalving (5.7 μ IU/mL), compared with d 0

to 7 postcalving and d 28 to 35 postcalving (3.6 and 3.7 μ IU/mL, respectively). Concentrations of NEFA and BHBA were lowest precalving (0.05 and 0.3 mmol/L, respectively), highest at d 0 to 7 postcalving (0.45 and 0.6 mmol/L, respectively), and intermediate at d 28 to 35 postcalving (0.27 and 0.5 mmol/L, respectively). Glucose concentrations were highest precalving (3.57 mmol/L), lowest at d 0 to 7 postcalving (3.26 mmol/L), and intermediate at d 28 to 35 postcalving (3.43 mmol/L), whereas urea concentrations were lowest precalving (3.38 mmol/L) compared with both d 0 to 7 postcalving and d 28 to 35 postcalving (4.56 and 4.56 mmol/L, respectively). Both plasma protein and albumin concentrations were greatest at d 28 to 35 postcalving (86.0 and 30.1 g/L, respectively), lowest at d 0 to 7 postcalving (79.5 and 28.6 g/L, respectively), and intermediate precalving (84.4 and 28.7 g/L, respectively). There was a genotype by stage of lactation interaction for insulin and plasma protein concentration. HighNZ had greater concentrations of insulin precalving with little difference in concentrations both at d 0 to 7 postcalving and at 28 to 35 d postcalving. All groups had similar plasma protein concentrations precalving and at 28 to 35 d postcalving but the LowNA group exhibited a greater reduction from precalving to d 0 to 7 postcalving and exhibited the greatest increase from d 0 to 7 postcalving and d 28 to 35 postcalving compared with both other groups.

The effects of genotype of HF and FS on blood metabolite and hormone concentrations at mating start date are summarized in Table 8. No significant interactions between genotype and FS were found and therefore, only main effects are reported. Genotype had no effect on insulin, NEFA, glucose, or plasma protein concentrations at mating start date. The HighNA group

Table 7. Effect of genotype (G) of Holstein-Friesian¹ and stage of lactation (S)² on plasma metabolite and hormone concentrations (back-transformed least squares means are presented in parentheses where appropriate)

Item	Prelactating			Calving			Postcalving			P-value		
	LowNA	HighNA	HighNZ	LowNA	HighNA	HighNZ	LowNA	HighNA	HighNZ	SE ³	G	S × G × S ⁴
Log _e Insulin (μIU/mL)	1.68 ^a (5.36)	1.70 ^a (5.46)	1.86 ^b (6.39)	1.31 ^c (3.71)	1.24 ^c (3.44)	1.25 ^c (3.50)	1.27 ^c (3.55)	1.37 ^c (3.92)	1.26 ^c (3.54)	0.047	0.61	<0.001
Log _e NEFA (mmol/L)	-3.04 (0.05)	-3.19 (0.04)	-2.96 (0.05)	-0.81 (0.45)	-0.85 (0.43)	-0.77 (0.46)	-1.36 (0.26)	-1.41 (0.24)	-1.19 (0.30)	0.062	0.001	<0.001
Log _e BHBA (mmol/L)	-1.13 (0.32)	-1.20 (0.30)	-1.20 (0.30)	-0.44 (0.64)	-0.48 (0.62)	-0.48 (0.62)	-0.67 (0.51)	-0.74 (0.48)	-0.68 (0.50)	0.039	0.26	<0.001
Glucose (mmol/L)	3.56	3.59	3.57	3.23	3.25	3.30	3.40	3.46	3.44	0.034	0.44	<0.001
Urea (mmol/L)	3.42	3.31	3.42	4.47	4.60	4.61	4.46	4.50	4.73	0.114	0.41	<0.001
Protein (g/L)	84.4 ^c	84.8 ^c	83.9 ^c	78.4 ^a	80.7 ^c	79.2 ^{ab}	87.0 ^{bcd}	86.6 ^d	84.6 ^{cd}	0.76	0.20	<0.001
Albumin (g/L)	28.6	29.1	28.6	28.2	28.9	28.8	29.9	30.3	30.0	0.02	0.18	<0.001

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

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Stage of lactation: precalving = 28–35 d precalving; calving = 0–7 d postcalving; postcalving = 28–35 d postcalving.

³SE = pooled standard error.

⁴Genotype by stage of lactation interaction.

had the greatest BHBA concentrations and HighNZ had the greatest urea concentration, whereas LowNA had the lowest albumin concentrations. Feeding additional concentrates in HC FS increased insulin and BHBA concentrations, whereas NEFA concentrations were reduced.

DISCUSSION

Agricultural reforms and milk quota deregulation within the EU is anticipated to result in a reduction in dairy farm numbers and an expansion in total production as farms increase scale (Hennessy and Thorne, 2006). Lips and Rieder (2005) projected that post-EU-milk-quota milk production in Ireland could increase by up to 39% but could be accompanied by a milk price reduction of up to 33%. Internationally, increased stocking rates and grazing intensity have been observed as the most important determinants of successful pastoral dairy farm production in an environment free from milk quotas (Journet and Demarquilly, 1979). Under such economic conditions, the development of systems based on efficiency of production, minimal cost, and maximum grass utilization will be of paramount importance (Shalloo et al., 2004; McCarthy et al., 2007b). Compared with classical Irish milk production systems derived for an EU milk quota scenario (Dillon et al., 1995; Horan et al., 2004), the implementation of more intensive management systems within the current experiment (characterized by the higher overall stocking density, increased grass utilization, and reduced concentrate supplementation, particularly within the MP FS) provide a unique opportunity to evaluate the likely effect of milk quota removal on the reproductive performance of various genotypes.

Under seasonal grass-based production systems, excellent herd fertility performance with compact calving at the start of the grass-growing season is of critical importance to maximize grass utilization and milk production efficiency. Overall reproductive efficiency for individual genotypes within the current study was suboptimal compared with target performances (Mee et al., 1999) or indeed compared with less intensive production systems operated under an EU milk quota scenario (Horan et al., 2004). Mean fertility performance measures were (target levels in parenthesis) 47% (60%) for pregnancy rate to first service, 61% (87%) for pregnancy rate after 42 d of breeding, and 80% (95%) for overall pregnancy rate.

Effect of Genetic Selection

Many studies have attempted to compare the fertility performance of cows of different genetic merit for milk

Table 8. Effect of genotype of Holstein-Friesian and feed system on plasma metabolite and hormone concentrations at mating start date (back-transformed least squares means are presented in parentheses where appropriate)

Item	Genotype (G) ¹			Feed system (F) ²		SE ³	P-value	
	LowNA	HighNA	HighNZ	MP	HC		G	F
Log _e Insulin (μIU/mL)	1.46 (4.30)	1.45 (4.25)	1.55 (4.74)	1.34 (3.84)	1.62 (5.10)	0.053	0.31	0.003
Log _e NEFA (mmol/L)	−1.57 (0.21)	−1.71 (0.18)	−1.64 (0.19)	−1.53 (0.21)	−1.75 (0.17)	0.066	0.31	0.02
Log _e BHBA (mmol/L)	−0.79 ^a (0.45)	−0.63 ^b (0.53)	−0.74 ^a (0.47)	−0.78 (0.46)	−0.65 (0.52)	0.032	0.002	0.01
Glucose (mmol/L)	3.36	3.45	3.40	3.39	3.41	0.033	0.24	0.68
Urea (mmol/L)	4.11 ^a	4.33 ^a	4.72 ^b	4.34	4.43	0.104	<0.001	0.45
Protein (g/L)	85.6	87.1	85.6	85.9	86.3	0.73	0.24	0.58
Albumin (g/L)	29.7 ^a	30.5 ^b	30.6 ^b	30.0	30.5	0.24	0.03	0.19

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

¹Genotype: LowNA = national average-genetic-merit North American Holstein-Friesian; HighNA = high-genetic-merit North American Holstein-Friesian; HighNZ = high-genetic-merit New Zealand Holstein-Friesian.

²Feed systems: MP = Moorepark; HC = high output per hectare.

³SE = pooled standard error.

production and, although some have found no association (Patton et al., 2007) or even a positive association (Buckley et al., 2003), the majority of studies have observed an antagonistic relationship between increased genetic merit for milk production and fertility performance. Experiments comparing cows of different levels of genetic merit for milk production have associated greater genetic merit for milk production with greater NEB in early lactation compared with cows of lower genetic merit for milk production (Veerkamp et al., 2003). These studies have invariably considered genetic merit exclusively within the context of milk production traits rather than total productive capacity (production plus reproduction and health). The use of overall breeding goals allows the genetic characteristics of Irish dairy cattle to be described in terms of productive, reproductive, calving, and health traits (Table 2; overall EBI and sub-indices). In the current study, the overall economic merit for milk production was similar for all 3 genotypes with most of the differential in overall EBI explained by differences in genetic merit for fertility performance rather than milk production. The superior reproductive performance observed within both HighNA and HighNZ is consistent with their higher genetic merit for fertility performance. The HighNA and HighNZ groups selected for greater fertility performance were more likely to be served earlier in the breeding season, have greater odds of being pregnant to first service and being pregnant after 42 d of the breeding season, and have a lower hazard of being culled than the LowNA group of lower merit for fertility performance. Within the North American HF context, the superior reproductive performance of HighNA compared with LowNA, despite a similar overall merit for milk production (pedigree index for milk volume and composition), further supports this hypothesis. The low levels of reproductive efficiency observed from industry statistics (submission rate after

24 d of the breeding season and 6-wk calving rate of 53 and 57%, respectively; ICBF, 2008) are similar to the results observed in the national average LowNA genotype. These results confirm both the important genetic contribution to this current sub-optimal performance and the urgent requirement for genetic progress within the national herd toward a more fertile animal for the future (McCarthy et al., 2007b).

Similar to the current study, Horan et al. (2004) observed superior fertility performance among HF cows of New Zealand ancestry within Irish pasture-based production systems and concluded that animals selected using a breeding index incorporating productive and reproductive traits under broadly similar pasture-based production systems may result in high fertility performance within Irish production systems. Unlike previous studies (Harris and Kolver, 2001; Horan et al., 2004), the results of the present study demonstrate that regardless of genetic origin, selection for increased milk production will not result in a deterioration in reproductive capacity if accompanied by increased genetic merit for fertility performance. The superior reproductive performance of HighNZ in this study compared with HighNA can be attributed to their higher overall genetic merit for fertility performance rather than to the geographical origin of the sires used.

Historical evidence linking increased milk production to inferior reproductive efficiency has been explained by an increased duration and intensity of NEB in early lactation (Butler and Smith, 1989). Similar to previous studies (Buckley et al., 2003), the reduced loss in body condition by HighNZ in early lactation is indicative of superior energy status and is consistent with the superior reproductive performance to first insemination. Although the potential economic value of milk production for all genotypes within the study is similar for all animals, the higher milk yield potential (pedigree index

for milk yield) of LowNA animals and the willingness to expend needed energy reserves to fuel an increased milk production capability to the detriment of other biological processes such as reproduction is evident in the current data set and consistent with the findings of Butler and Smith (1989). Similarly, HighNA animals with high milk yield potential exhibited similar losses in body condition from calving to the start of the breeding season; however, maintaining a greater BCS than LowNA animals at mating start date resulted in superior reproductive performance.

The relationships between blood parameters and fertility have been well documented where NEB is associated with decreased concentrations of glucose and insulin and increased concentrations of NEFA (Butler, 1998). Despite the increase in stocking intensity within this study compared with previous EU-milk-quota-based systems (Dillon et al., 1995; Horan et al., 2004), changes in blood metabolites around calving and prebreeding were within normal ranges and similar to results observed by McCarthy et al. (2007a). However, concentrations of NEFA were greater in HighNZ animals at 28 to 35 d postcalving, which is inconsistent with the reduced loss in body condition observed by these animals during the same period. Furthermore, at breeding, genotype had a significant effect on BHBA, urea, and albumin concentrations; however, these differences were also inconsistent. This suggests that, although intrinsic differences in blood metabolites may exist between diverse genetic groups, these differences are not responsible for the observed differences in reproductive performance. The results of the current study demonstrate that animals of similar genetic merit for milk production traits can have significantly different fertility performance without exhibiting significant differences in metabolic blood profiles. These results are in agreement with the findings of Patton et al. (2007) and illustrate that the studied plasma metabolite concentrations in early lactation or during the breeding season are not a useful predictor of reproductive performance outcomes.

Effect of Feeding System

In addition to genetic factors, animal performance differences may often relate to differences in environmental factors such as nutrition, health, and management. Although many studies have been carried out to examine the effect of diet on reproductive performance, particularly within NA HF dairy cows with high merit for milk production (Buckley et al., 2000; Horan et al., 2004), few studies have observed significant improvements in fertility performance in pasture-based systems through increased supplementation (Beever, 2004). The MP FS in the current experiment was designed

to increase milk production through increased pasture utilization, as evidenced by increased grazing intensity and lower overall feed allocation compared with current typical EU-milk-quota-based systems (Horan et al., 2004). The HC FS was created to increase overall dietary intake above MP FS levels using additional concentrates throughout lactation while achieving similar high levels of pasture utilization. The experimental hypothesis tested was that, within intensive production systems, improving energy status through increased feed intake in HC FS would result in superior reproductive performance. However, no significant FS effect or interaction between genotype and FS was observed in this study, and similar to previous experiments in Ireland (Horan et al., 2004) and internationally (Koliver et al., 2005), incremental increases in total DM intake did not improve reproductive performance. The improved energy status of the HC FS is further evidenced by lower NEFA and BHBA concentrations as well as by the reduction in BCS change between calving and mating start date. As all animals were treated similarly during the dry period, there was no carryover effect of FS from the previous lactation on blood metabolites precalving, around parturition, or 28 to 35 d postcalving. Similar to the findings of Horan et al. (2004), these results suggest that offering higher levels of concentrate supplementation does not alleviate the reduced reproductive performance of animals of low genetic merit for reproductive traits. These results also suggest that although concentrate supplementation does alleviate loss in body condition in early lactation and results in animals of higher BCS throughout lactation, increasing BCS within a FS has no effect on reproductive performance outcomes.

CONCLUSIONS

Genotype had a significant effect on reproductive performance in the current study. Both the HighNA and HighNZ genotypes, selected for superior reproductive performance, had superior submission rates and pregnancy rates and exhibited greater survival than the average genetic merit (LowNA) genotype. The lack of an FS effect or interaction between genotype and FS for reproductive traits suggests that offering higher levels of concentrate supplementation to negate NEB or improve BCS does not alleviate the reduced reproductive performance of animals of inferior genetic merit for fertility traits. The results do suggest that genetic differences in BCS evident within an FS are an effective means to predict efficiency of fertility performance. These results further substantiate the use of multitrait selection indexes such as the EBI to derive animals with superior milk production and reproductive performance characteristics.

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