Genetic and nongenetic factors associated with lactation length in seasonal-calving, pasture-based dairy cows

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ABSTRACT

Lactation yield estimates standardized to common lactation lengths of 270-d or 305-d equivalents are commonly used in management decision support tools and dairy cow genetic evaluations. The use of such measurements to quantify the (genetic) merit of individual cows fails to penalize cows that do not reach the standardized lactation length, or indeed reward cows that lactate for more than the standardized lactation length. The objective of the present study was to quantify the genetic and nongenetic factors associated with lactation length in seasonal-calving, pasture-based dairy cows. A total of 616,350 lactation length records from 285,598 Irish cows were used. Linear mixed models were used to quantify the associations between lactation length and calving month, parity, age at calving, previous dry period length, calving difficulty score, heterosis, recombination loss, breed, and herd size, as well as to estimate the genetic and residual variance components of lactation length. The median lactation length in the edited data set was 288 d, with 27% of cows achieving lactations of at least 305 d. Relative to cows calving in January, the lactations of cows calving in February, March, or April were, on average, 4.2, 12.7, and 21.9 d shorter, respectively. The lactation length of a first parity cow was, on average, 7.8, 8.6, and 8.4 d shorter than that of second, third, and fourth parity cows, respectively. Norwegian Red and Montbéliarde cows had, on average, a 4.7- and 1.6-d shorter lactation than Holstein-Friesian cows, respectively. The heritability estimate, coefficient of genetic variation, and repeatability estimate of lactation length were 0.02, 1.2%, and 0.04, respectively. Based on the genetic standard deviation for lactation length estimated in the present

study (3.3 d), cows ranked in the top 20% for genetic merit for lactation length would be expected to have lactations 9.2 d longer than cows in the bottom 20%, demonstrating exploitable genetic variability. Given the vast array of genetic and nongenetic factors associated with lactation length, an approach which combines improved management practices and selective breeding may be an efficient and effective strategy to lengthen lactations.

Key words: lactation length, spring-calving, pasture-based, management factors, genetic parameters

INTRODUCTION

Lactation yield estimates standardized to a common lactation length are almost exclusively used in both management decision support tools and dairy cow genetic evaluations (Quist et al., 2007). Commonly used standardized lactation lengths are those to 305-d equivalents (Olori et al., 1999) or 270-d equivalents (Harris and Winkelman, 2004), with the former often standardized further to a mature equivalent (Marti and Funk, 1994). The use of such standardized metrics to quantify the (genetic) merit of individual cows, however, often fails to fully penalize cows that (consistently) do not reach the standardized lactation length (i.e., cows that naturally dried off prematurely), and likewise fails to reward animals that lactate for more than 270 or 305 d. Substantial variability in lactation length has been reported in both Holstein cows (Hossein-Zadeh, 2012) and Holstein-Friesian cows (Evans et al., 2006; Van Eetvelde et al., 2017). Nonetheless, limited research exists on the factors associated with lactation length in dairy cows. Indeed, where studies have been conducted, they have generally been restricted to cows in confinement systems (Tiezzi et al., 2012; Weber et al., 2015) or tropical regions (Bajwa et al., 2004; Hossein-Zadeh, 2012).

Factors previously identified as being associated with lactation length in dairy cows include parity (Hossein-

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Zadeh, 2012), age at calving within parity (Bajwa et al., 2004), season of calving (Bajwa et al., 2004), inadequate milk yield in late lactation (Weber et al., 2015), and poor fertility (Tiezzi et al., 2012; Weber et al., 2015). Hossein-Zadeh (2012) reported that first parity Iranian Holstein cows had a 16-d and 23-d longer lactation compared with second and third parity cows, respectively. A strong positive genetic correlation between lactation length and interval from first service to conception has been reported by Tiezzi et al. (2012), suggesting that extended lactations may be a consequence of poor fertility in year-round calving confinement systems.

Nonetheless, factors previously documented to associate with lactation length in confinement systems may not reflect those associated with lactation length in seasonal-calving systems. Seasonal-calving systems are characterized by all cows calving in a concentrated period of the year (Macdonald et al., 2008; Berry et al., 2013) as well as being dried off in a relatively short period. In the 5 yr before 2019, inclusive, approximately 70% of Irish cows calved between January and March each year (ICBF, 2019). Hence, poor fertility (i.e., calving later in the season) in a seasonal-calving system should negatively affect lactation length. Should cows fail to achieve a lactation length of 305 d, their actual yield may be less than their reported standardized yield. Given the reliance on standardized milk yield for management decisions and genetic evaluations, determining the factors associated with lactation length is of significant importance. Therefore, the objective of the present study was to identify the genetic and nongenetic factors associated with lactation length in a seasonal pasture-based dairy cow production system.

MATERIALS AND METHODS

All Irish dairy producers are legally required to inform the Irish Department of Agriculture, Food and the Marine of certain details relating to calving events, including the date of birth and unique dam identifier. Producers must also legally record all animal deaths and interlocation movements. This information is shared with the Irish Cattle Breeding Federation (ICBF) and held in the national database. Additional information including dry-off dates, test-day milk yield and composition, as well as calving difficulty scores are recorded on a voluntary basis and provided to the ICBF. All the above information was downloaded from the pre-existing ICBF national database for the purpose of this study; therefore, it was not necessary to obtain animal ethics committee approval in advance of conducting this study.

Data Edits

Dairy herds were defined as spring-calving if >70% of cows calved between the months of January and June, inclusive (Ring et al., 2019); only spring-calving herds, which are the predominant system in Ireland (Berry et al., 2013), were retained. Calving dates and dry-off dates were available for 3,070,479 lactations from 1,265,504 cows calving in 9,748 spring-calving herds between the years 2008 and 2017, inclusive. Lactation length was calculated as the number of days between calving and recorded dry-off; culling dates were not used in the derivation of lactation length and only 3.8% of the cows in the herds retained were culled with no recorded dry-off date. Records where the cow parity was >10 or lactation length was >730 d (or both) were discarded, as were cows without a known sire. First parity cows recorded to have calved younger than 600 d of age were also removed. Further to this, the median age at calving was calculated for each parity; 432,949 parity records where the cows calved more than 180 d before or after the median age at calving within parity were not considered further. For all remaining records, age at calving was categorized, within parity, into 6 groups, each 60 d in duration, relative to the median age at calving within parity. Where a dry-off date in the preceding lactation was available, the dry period length before the commencement of lactation was calculated. Dry periods ≤ 14 d or > 112 d were removed and the remaining dry periods were categorized into 5 groups: > 14 to ≤ 35 d, > 35 to ≤ 56 d, > 56 to ≤ 77 d, > 77 to ≤ 98 d, and > 98 to ≤ 112 d; the frequency per class was 1.3%, 9.6%, 35.8%, 37.0%, and 16.3%, respectively. Missing previous dry period length records (e.g., first lactation cows) or where a dry-off date was not recorded in the previous lactation were coded separately to facilitate their inclusion in the subsequent statistical analyses. Herd size was categorized into 5 groups, in intervals of 50 cows, from ≤ 50 cows calving in a given year to > 250 cows calving in a given year. Heterosis and recombination loss coefficients were calculated for each cow as described by Ring et al. (2018). Heterosis was divided into 12 classes (0%, $> 0\%$ and $\leq 10\%$, $> 10\%$ and $\leq 20\%$, $> 20\%$ and $\leq 30\%$, $> 30\%$ and $\leq 40\%$, $> 40\%$ and $\leq 50\%$, $> 50\%$ and $\leq 60\%$, $> 60\%$ and $\leq 70\%$, $> 70\%$ and $\leq 80\%$, $> 80\%$ and $\leq 90\%$, $> 90\%$ and $\leq 99\%$, and $> 99\%$). Recombination loss was divided into 7 classes (0%, $> 0\%$ and $\leq 10\%$, $> 10\%$ and $\leq 20\%$, $> 20\%$ and $\leq 30\%$, $> 30\%$ and $\leq 40\%$, $> 40\%$ and $\leq 50\%$, and $> 50\%$). Calving difficulty was subjectively recorded by producers on a scale of 1 to 4, in which 1 = no assistance required during calving, 2 = assistance provided with some calving difficulty, 3 = assistance provided with

considerable calving difficulty, but no veterinary intervention, and 4 = assistance provided with considerable calving difficulty resulting in veterinary intervention. Lactations with no calving difficulty score were coded separately to facilitate their inclusion in the statistical analyses.

For the purpose of subsequent analyses, the edited data set was stratified by month of calving as January, February, March, and both April and May combined (due to the fact that there were fewer calving events in these months because of the seasonal nature of calving in Ireland; Berry et al., 2013); records relating to cows calving in June were removed as, on average, <3% of Irish cows calve in June (ICBF, 2019). Within each month of calving, animals were assigned to a contemporary group, based on calving date. The algorithm used to generate contemporary groups was that used in the Irish national genetic evaluations (Berry et al., 2013). Animals that calved in the same herd and month within 10 d of each other were initially clustered together. Where <10 animals were clustered together, these animals were grouped with an adjacent contemporary group in time within the same herd and calving month until each contemporary group contained ≥ 10 records. Records from contemporary groups with <10 animals were removed. Cow records from 1,078 herds with at least one contemporary group represented in each of the calendar months of January, February, and March, as well as the combined calendar months of April and May, across the period of the present study were retained. Following these edits, 109,988 records from 80,390 cows calving in January, 327,023 records from 193,402 cows calving in February, 121,358 records from 97,802 cows calving in March, and 30,554 records from 27,666 cows calving in April or May were available for analyses.

For the identification of the phenotypic factors associated with lactation length, all data from the 1,078 herds were retained but an alternative contemporary group was regenerated. Using the contemporary group algorithm already defined (Berry et al., 2013), contemporary groups were assigned within herd, across calving

months, with a maximum distance between the calving dates of 60 d. Following the removal of contemporary groups with <10 records, 616,350 records from 285,598 cows in 1,078 herds remained.

To estimate the variance components of lactation length within individual calving months, a random sample of 50% of the 1,078 herds represented in all calving month subsets, with assigned contemporary groups, were retained for January, February, and March; given the limited number of calving events available for April and May, all records were retained for these months. Following all edits, 56,858 records from 41,479 cows calving in January, 169,603 records from 99,878 cows calving in February, 61,889 records from 49,813 cows calving in March, and 30,554 records from 27,666 cows calving in April or May were retained for genetic analyses (Table 1). For a separate analysis to estimate variance components of lactation length across calving months, the records retained from each calving month were combined. A random sample of 20% of the herds represented in all calving months was retained; 58,565 records for 27,955 cows in 108 herds remained. Pedigree information for all animals was traced back to the founder animals and founders were assigned to 11 genetic groups based on breed.

Lactation Length Phenotypes

Six different phenotypes representing alternative measures of lactation length were defined. One continuous trait was defined as lactation length where the lactation length was restricted to be ≤ 365 d. Preliminary analyses revealed minimal differences in model solutions or variance components when lactations ≤ 365 d in length were considered, lactations between 100 and 365 d in length were considered, or indeed when lactations of all lengths were considered. Five binary lactation length variables were also defined based on whether (i.e., coded as one) or not (i.e., coded as zero) the lactation length reached a given length, which, in the present study, was set at 150 d (**LL150**), 200 d (**LL200**), 240 d (**LL240**), 270 d (**LL270**), or 305 d

Table 1. Number of records, cows, and herds, as well as the mean and median lactation length, genetic standard deviation (σ_g), heritability (h^2 ; SE in parentheses), and repeatability (t ; SE in parentheses) of lactation length when restricted to ≤ 365 d for cows calving in January, February, March, and April and May, as well as all 5 calendar months combined

Item	Records	Cows	Herds	Mean	Median	σ_g	h^2	t
All months	58,565	27,955	108	286.1	288.0	3.29	0.022 (0.004)	0.039 (0.005)
January	55,164	40,188	539	303.5	305.0	3.43	0.025 (0.005)	0.053 (0.009)
February	166,454	97,773	539	289.4	290.0	3.24	0.024 (0.003)	0.061 (0.004)
March	60,217	48,437	539	269.0	268.0	3.14	0.018 (0.004)	0.018 (0.004)
April and May	27,850	25,289	1,078	251.7	250.0	3.21	0.013 (0.006)	0.013 (0.006)

(LL305); that is, if a cow had a code of 1 for LL305, it also had a code of 1 for LL150, LL200, LL240, and LL270.

Statistical Analyses

Phenotypic Analyses. The associations between lactation length variables and fixed effects were quantified using linear mixed models in ASReml (Gilmour et al., 2009). Both cow and contemporary group were fitted as random effects.

$$\begin{aligned} \text{LL}_{ijklmnopqrstu} = & \text{Het}_j + \text{Rec}_k + \text{Herd size}_l \\ & + \text{Dry period length}_m + \text{Calving difficulty score}_n \\ & + \text{Age}_o | \text{Parity}_p + \text{Calving month}_q \left| \sum_{u=1}^2 \text{Calving day}^u \right. \\ & + \sum_{r=1}^6 \text{Breed}_r + \text{CG}_s + \text{Cow}_t + e_{ijklmnopqrstu}, \end{aligned}$$

where $\text{LL}_{ijklmnopqrstu}$ was the lactation length phenotype for animal i ; Het_j was the fixed effect for heterosis class j ($j = 0$ to 11); Rec_k was the fixed effect for recombination loss class k ($k = 0$ to 6); Herd size_l was the fixed effect for herd size class l ($l = 1$ to 5); $\text{Dry period length}_m$ was the fixed effect of the previous dry period length class m ($m = 1$ to 6); $\text{Calving difficulty score}_n$ was the fixed effect of calving difficulty score n ($n = 1$ to 4); $\text{Age}_o | \text{Parity}_p$ was the fixed effect of the interaction between age at calving o and parity p ($o = 1$ to 6, $p = 1$ to 10); $\text{Calving month}_q \left| \sum_{u=1}^2 \text{Calving day}^u \right.$ was the fixed effect of the interaction between calving month q and calving day relative to the contemporary group median; $\sum_{r=1}^6 \text{Breed}_r$ was the breed proportion r of the animal i fitted as a linear covariate representing for all of the main dairy breeds separately (i.e., Jersey, Ayrshire, Brown Swiss, Montbéliarde, Norwegian Red, and Normande) except Holstein-Friesian; CG_s was the random effect of contemporary group s , where $\text{CG}_s \sim N(0, \mathbf{I}\sigma_{\text{CG}}^2)$ and σ_{CG}^2 represents the contemporary group variance and $\mathbf{I}$ the identity matrix; Cow_t was the random cow effect across lactations where $\text{Cow}_t \sim N(0, \mathbf{I}\sigma_{\text{cow}}^2)$ and σ_{cow}^2 represents the cow variance and $\mathbf{I}$ the identity matrix, and $e_{ijklmnopqrstu}$ was the residual term where $e \sim N(0, \mathbf{I}\sigma_e^2)$ and σ_e^2 represents the residual variance and $\mathbf{I}$ the identity matrix.

Estimation of Variance Components. The genetic and residual variance components for all lactation length phenotypes were estimated using linear mixed models in ASReml (Gilmour et al., 2009) for each month of calving individually as well as for all months of calving combined. The linear model fitted to each month separately was

$$\begin{aligned} \text{LL}_{ijklmnopq} = & \text{CG}_j + \text{Het}_k + \text{Rec}_l + \text{Age}_m | \text{Parity}_n \\ & + \text{Dry period length}_o + \sum_{p=1}^2 \text{Calving day}^p + a_i + pe_q \\ & + e_{ijklmnopq}, \end{aligned}$$

where $\text{LL}_{ijklmnopq}$ was the observed lactation length phenotype for animal i ; CG_j was the fixed effect for contemporary group j ; Het_k was the fixed effect for heterosis class k ($k = 0$ to 11); Rec_l was the fixed effect for recombination loss class l ($l = 0$ to 6); Age_m was the fixed effect for age at calving class m ($m = 1$ to 6); Parity_n was the fixed effect for parity n ($n = 1$ to 10); $\sum_{p=1}^2 \text{Calving day}^p$ was the linear and quadratic fixed effect for calving day relative to the contemporary group median calving day; $\text{Dry period length}_o$ was the fixed effect for previous dry period length class o ($o = 1$ to 6); a_i was the additive random effect of animal i where $a \sim N(0, \mathbf{A}\sigma_a^2)$ and σ_a^2 represents the genetic variance and $\mathbf{A}$ the numerator relationship matrix; the pedigree of all animals was traced back to their founder animals and allocated to genetic groups based on breed to construct the numerator relationship matrix; pe_q was the random animal permanent environmental effect across lactations where $pe_q \sim N(0, \mathbf{I}\sigma_{pe}^2)$ and σ_{pe}^2 represents the permanent environmental variance and $\mathbf{I}$ the identity matrix and $e_{ijklmnopq}$ was the residual term, where $e \sim N(0, \mathbf{I}\sigma_e^2)$ and σ_e^2 represents the residual variance and $\mathbf{I}$ the identity matrix. The heritability estimates for the binary lactation length phenotypes were transformed from the observed scale to the underlying liability scale using the percentage of cows achieving each trait enabling the comparison of heritability estimates between traits (Robertson and Lerner, 1949).

Genetic Evaluation

To estimate the genetic trend for lactation length in Irish seasonal-calving, pasture-based dairy cows, additional lactation records from cows born since 2000 and

Table 2. Breed covariate solutions (SE in parentheses) of the 6 dairy breeds, Jersey (JE), Ayshire (AY), Brown Swiss (BS), Montbéliarde (MO), Norwegian Red (NR), and Normande (NO), relative to Holstein-Friesian for lactation length restricted to ≤ 365 d (LL365) and lactation length defined as a binary trait ≥ 150 d (LL150), ≥ 200 d (LL200), ≥ 240 d (LL240), ≥ 270 d (LL270), and ≥ 305 d (LL305)

Item	JE	AY	BS	MO	NR	NO
LL365	-0.07 (0.37)	0.31 (1.69)	-2.62 (2.03)	-1.56** (0.59)	-4.73*** (0.51)	-2.51 (4.54)
LL150	0.003** (0.001)	0.001 (0.004)	-0.009 (0.005)	-0.001 (0.001)	0.001 (0.001)	-0.007 (0.012)
LL200	0.004** (0.001)	0.001 (0.007)	-0.022** (0.008)	0.001 (0.002)	0.003 (0.002)	-0.014 (0.019)
LL240	0.000 (0.003)	-0.011 (0.013)	-0.005 (0.016)	0.001 (0.005)	-0.020*** (0.004)	0.000 (0.036)
LL270	-0.008* (0.005)	0.005 (0.023)	-0.025 (0.027)	-0.027*** (0.008)	-0.043*** (0.006)	-0.068 (0.007)
LL305	0.009 (0.025)	0.043 (0.030)	0.043 (0.030)	-0.029* (0.009)	-0.060*** (0.008)	-0.019 (0.007)

Significance of the difference from Holstein-Friesian (i.e., zero): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

calving before the end of 2017 were obtained from the ICBF national database. All edits applied previously were imposed as was the statistical model developed and the variance components estimated in the present study. Contemporary group was defined within calving month, with records from April and May combined. A total of 1,678,070 lactation records from 817,625 cows remained. Pedigree information for all animals was traced back to the founder animals and founders were assigned to genetic groups based on breed. Individual animal EBV for lactation length were calculated using the MIX99 software suite (Strandén and Lidauer, 1999). The genetic trend by year of birth for lactation length was estimated for all Holstein-Friesian females (572,981 cows) with lactation length records as well as separately for 6,327 Holstein-Friesian male animals born since 2000 with ≥ 10 (grand)progeny with lactation length records.

RESULTS

Of the 616,350 records from milk recorded herds used in the phenotypic analyses, 20.1%, 53.6%, 20.5%, 4.9%, and 0.9% of the cows calved in January, February, March, April, and May, respectively. The median lactation length in the edited data set was 288 d; before edits, the median lactation length was 280 when lactation length was restricted to ≤ 365 d. Whereas 27% of cows achieved a target lactation length of 305 d, 76% of cows achieved a lactation length of 270 d. February 14 was the median calving day of the year in the edited data set, with 41% of the cows in the data set calving between February 4 and 24. Before edits, the median calving date was February 23. The median dry-off date was November 26, with 37% of cows being dried off between November 16 and December 6. Before edits, the median dry-off date was November 25.

Phenotypic Risk Factors

Except for recombination loss and some breed covariates, all the fixed effects included in the phenotypic

model were associated ($P < 0.05$) with the continuous dependent variable of lactation length. When lactation length was defined as a binary trait, all fixed effects included in the phenotypic models were associated with lactation length with the exception of the interaction between calving day and calving month when lactation length was defined as LL150, heterosis coefficient when lactation length was defined as LL200, and recombination loss coefficient when lactation length was defined as LL270. The model solutions for each breed covariate associated with each binary lactation length trait are detailed in Table 2.

Month of Calving, Parity, and Age at Calving.

Relative to cows calving in January, the lactation of a cow calving in February, March, April, or May was 4.2, 12.7, 21.9, and 33.7 d shorter, respectively (Figure 1). For cows calving in January, the likelihood of achieving LL150, LL200, LL240, LL270, and LL305 was 0.5%, 8.1%, 26.2%, 42.4%, and 63.1% higher, respectively, than for cows calving in May (Figure 2); the percentage change in likelihood of achieving each binary trait was calculated by dividing the model solution for the class of interest (calving in May) by the model solution for the population mean. A first parity cow had a 7.8, 8.6, and 8.4 d shorter lactation than a second, third, and fourth parity cow, respectively (Figure 1). Ninth parity cows were the least likely to achieve LL150 and first parity cows were the least likely to have lactations of ≥ 305 d relative to cows in second, third, fourth, or fifth parity (Figure 2). Cows calving 121 to 180 d beyond the parity median lactated for 5.3 additional days (Figure 1) and were more likely to lactate ≥ 305 d compared with cows calving 120 to 180 d earlier than their parity median (Figure 2). Relative to cows calving 120 to 180 d older than the parity median age at calving, cows calving 120 to 180 d younger than the parity median were the least likely to lactate for at least 305 d.

Breed, Heterosis, and Recombination Loss Coefficient. Norwegian Red and Montbéliarde cows had, on average, a 4.7 and 1.6 d shorter lactation, respectively, than Holstein-Friesian cows (Table 2). The likelihood of achieving LL150 was 0.26% greater in Jersey

Figure 1. The change in lactation length (LL; standard error bar represents ± 1 SE) associated with (A) calving month relative to cows calving in January, (B) parity relative to first parity cows, (C) age at calving relative to cows calving between 180 and 120 d earlier than the parity median, (D) heterosis coefficient relative to cows with a heterosis coefficient of 0%, (E) calving difficulty score relative to cows with a calving difficulty score of 1, (F) dry period length relative to cows with a dry period of between 15 and 35 d, and (G) herd size relative to herds with ≤ 50 cows.

Figure 2. The association between the change in the percentage that achieved lactation length ≥ 150 d ($\blacklozenge$), ≥ 200 d ($\blacksquare$), ≥ 240 d ($\blacktriangle$), ≥ 270 d ($\times$), ≥ 305 d ($\square$) and (A) calving month relative to cows calving in January, (B) parity relative to first parity cows, (C) age at calving relative to cows calving between 180 and 120 d earlier than the parity median, (D) heterosis coefficient relative to cows with a heterosis coefficient of 0%, (E) recombination loss coefficient relative to cows with a recombination loss coefficient of 0%, (F) calving difficulty score relative to cows with a calving difficulty score of 1, (G) dry period length relative to cows with a dry period of between 15 and 35 d, and (H) herd size relative to herds with ≤ 50 cows. Standard error bar represents ± 1 SE unit.

Figure 3. The genetic trend by year of birth for lactation length estimated for Holstein-Friesian cows (■), and Holstein-Friesian males with ≥ 10 (grand)progeny with lactation length records (◆).

cows relative to Holstein-Friesian cows. The likelihood of achieving LL200 was 0.45% greater and 2.2% less in Jersey cows and Brown Swiss cows, respectively, than their Holstein-Friesian contemporaries. A Norwegian Red cow had a lower likelihood of achieving LL240 than a Holstein-Friesian cow. Relative to Holstein-Friesian cows, Jersey cows, Montbéliarde cows, and Norwegian Red cows were less likely to achieve LL270, respectively (Table 2). Norwegian Red cows and Montbéliarde cows were also less likely to achieve LL305 relative to Holstein-Friesians (Table 2).

Cows with a heterosis coefficient of 0% had a 0.95 d longer lactation, a lower likelihood of achieving LL150 and LL200, and a higher likelihood of achieving LL270 and LL305 relative to cows with a heterosis coefficient of between 91% and 99% (Figures 1 and 2). Cows with a heterosis coefficient of $>99\%$ had the highest likelihood of achieving LL240 relative to cows with a heterosis coefficient of 0% (Figure 2).

Cows with a recombination loss coefficient of between 41% and 50% had a higher likelihood of achieving LL150 and LL200 relative to cows with a recombination loss coefficient of between 1% and 10%. Cows with a recombination loss coefficient of $>50\%$ were more likely

to achieve LL240 relative to cows with a recombination loss coefficient of 1% to 20%. Having a recombination loss coefficient of 1% to 10% was associated with an improvement in achieving LL305 relative to cows with a recombination loss coefficient of 0% (Figure 2).

Calving Difficulty, Dry Period Length, and Herd Size. Cows that received veterinary assistance at calving lactated, on average, for an additional 0.9 d (Figure 1) relative to a cow calving with a score of 2 (assistance provided with some calving difficulty). Cows that received veterinary assistance at calving were more likely to lactate for at least 270 or 305 d, respectively, relative to a cow calving without any recorded difficulty (Figure 2). Conversely, cows calving without any recorded calving difficulty were more likely to reach 150 and 200 d in lactation relative to cows calving with difficulty (Figure 2).

Relative to cows with a dry period of between 15 and 35 d, cows with a dry period of between 36 and 56 d had a 3.3 d longer lactation and were more likely to have lactations at least 150, 200, or 240 d (Figures 1 and 2). Cows with a dry period of between 99 and 112 d were less likely to lactate for at least 270 or 305 d, respectively, relative to cows with dry period of >36 to ≤ 56 d.

Lactation length was, on average, 6 d (SE = 0.8 d) shorter in herds with >200 cows relative to herds with ≤ 50 cows calving a year (Figure 1). Similarly, the largest herds had a lower likelihood of lactating for at least 150, 200, 240, 270, and 305 d compared with herds with ≤ 50 cows (Figure 2).

Genetic Parameters

The genetic standard deviation, heritability, and repeatability estimates of lactation length were 3.29 d, 0.022, and 0.039, respectively, when data from all calving months were analyzed together (Table 1) and the lactation length was defined as a continuous trait. When calving months were analyzed separately, the genetic standard deviation, heritability, and repeatability

Table 3. The percentage achieved as well as the genetic standard deviation (σ_g), heritability estimate (h^2 ; SE in parentheses), repeatability (t; SE in parentheses), and heritability estimate on the underlying liability scale (h^2_L) of binary lactation length traits: lactation length ≥ 150 d (LL150), ≥ 200 d (LL200), ≥ 240 d (LL240), ≥ 270 d (LL270), and ≥ 305 d (LL305)

Item	Percentage achieved, %	σ_g	h^2	t	h^2_L
LL150	99.61	0.003	0.0021 (0.0014)	0.0021 (0.0014)	0.061
LL200	98.95	0.004	0.0023 (0.0017)	0.0062 (0.0053)	0.031
LL240	94.64	0.018	0.0097 (0.0032)	0.0146 (0.0051)	0.044
LL270	75.96	0.037	0.0138 (0.0035)	0.0418 (0.0049)	0.026
LL305	27.24	0.029	0.0073 (0.0023)	0.0073 (0.0023)	0.013

estimates of lactation length ranged from 3.1 to 3.4 d, from 0.013 to 0.025, and from 0.013 to 0.061, respectively (Table 1). The coefficient of genetic variation for lactation length was 1.2% and did not vary by more than 0.16 percentage units across the different calving months. The coefficient of genetic variation, calculated as described by Burdon (2008), for the binary traits ranged from 4.9% and 8.7%. When binary lactation length traits were analyzed by calving month, the heritability estimates for all traits on the underlying liability scale were lowest for cows calving in April and May except for LL200. LL270 was the most repeatable trait apart from cows calving in April and May when LL150 was the most repeatable trait (Table 3; Supplemental Table S1, <https://doi.org/10.3168/jds.2020-18941>). In addition to frequently being the most repeatable trait, LL270 had the greatest coefficient of genetic variation relative to all other binary lactation length traits.

Genetic Evaluation

With the exception of a small reduction in the mean EBV for lactation length in cows born in 2009 relative to cows born in 2008, the mean EBV for lactation length of Holstein-Friesian cows increased year on year (Figure 3). The EBV for lactation length of a Holstein-Friesian cow born in 2015 was, on average, 3.75 d higher than the EBV of a cow born in 2000. The average increase in the EBV for lactation length, estimated from a linear regression model fitted through the mean annual EBV, was 0.25 d/yr for Holstein-Friesian cows. The trend in the EBV for lactation length of Holstein-Friesian males born after 2000 increased, on average, by 0.09 d/yr.

DISCUSSION

The profitability of the Irish dairy industry, as with any in situ grazing-based production system, is fundamentally reliant on compact seasonal calving just before the initiation of grass growth (Dillon et al., 2003). This is reflected in the median calving date and dry-off date of cows in the edited data set being February 14 and November 26, respectively. Although achieving lactations of 305 d ensures the recommended 60-d dry period (Capuco et al., 1997), it also enables the maintenance of the crucial 365-d calving interval. Additionally, if lactations of 305 d were achieved, the standardized yields currently used in dairy cow genetic evaluations and management decision support tools would be more reflective of actual milk yield. Nevertheless, the median lactation length of Irish dairy cows in the edited data set used in the present study was 288 d, which is low relative to most

international estimates (Hossein-Zadeh, 2012; M'hamdi et al., 2012), particularly in first lactation cows (Van Eetvelde et al., 2017). This shortened lactation length is likely due to differences in the constraints imposed in seasonal pasture-based production systems versus confinement systems. In line with this, mean lactation length calculated from tanker collection information in New Zealand, which also operates a seasonal-calving, pasture-based dairy production system, was 271 d (LIC and DairyNZ, 2019). The fact that only 27% of cows in the present study achieved lactations of 305 d implies that there is significant scope to improve the average lactation length of pasture-based dairy cows, but also that the often quoted standardized 305-d yield may be an overestimate for many. Using the parameters of a lactation function fitted to the yield of 3 genotypes of Irish dairy cows as presented by Horan et al. (2005), it was possible to calculate daily yield and deduce the loss in yield with a 288-d lactation versus a 305-d lactation. For the 3 genotypes, the yield in the first 288 d of lactation was 97.1% to 97.5% that of the respective 305-d yield. Whereas limited research has been undertaken to quantify the associations between both genetic and nongenetic factors with lactation length in confinement systems (Tiezzi et al., 2012), no equivalent studies exist for pasture-based, seasonal-calving temperate dairy production systems. The motivation for the present study was to fill this void.

Management Factors

The plethora of management factors associated with lactation length in the present study represents opportunities to lengthen lactations, but also a checklist for extension officers when exploring why a given herd has relatively short lactations. Given the large differences in lactation length associated with calving month, increasing the proportion of the herd calving in earlier months would be advantageous to lengthen lactations. This large impact is a function of seasonal-calving systems where all cows tend to be dried off in early winter, regardless of the previous or the subsequent predicted calving date. Increasing the proportion of the herd calving earlier in the year could be achieved through optimized reproductive management together with astute breeding decisions. Excellent reproductive performance is therefore key; considerable gains in performance have been achieved in most global dairy cow populations owing to genetic gain achieved following the consideration of reproductive performance in dairy cow breeding goals (Berry et al., 2014; Ma et al., 2019). In Ireland, for example, between the years 2010 and 2018, inclusive, there was an 8.2 percentage unit

increase in the proportion of Irish dairy cows calving in January and February (ICBF, 2019). The emphasis on compact seasonal calving, corresponding to the commencement of grass growth, is replicated in other pasture-based systems (Macdonald et al., 2008) but not in confinement systems where year-round calving is more the norm. Therefore, since previous studies were based on tropical and confinement systems, before the present study, calving month had not been considered as a factor associated with lactation length. The closest comparable trait to calving month in a confinement system is season of calving and this indeed has been documented to be associated with lactation length in dairy herds (Bajwa et al., 2004; M'hamdi et al., 2012; Hossein-Zadeh, 2013). Nonetheless, the association between season of calving and lactation length in confinement systems may reflect more seasonal feeding regimens, changes in ambient temperatures, or other seasonal factors rather than management practices per se.

In contrast to calving month, the association between parity and lactation length has been reported extensively (Hossein-Zadeh, 2012; M'hamdi et al., 2012; Hossein-Zadeh, 2013). Although frequently associated with shorter lactations in confinement systems (M'hamdi et al., 2012; Hossein-Zadeh, 2013), older cows, on average, had longer lactations in the present study. The difference in the association between increasing parity and lactation length in the present study relative to previous studies (M'hamdi et al., 2012; Hossein-Zadeh, 2013) may be dependent on diet, location, or production system. Cows are often dried off early due to low milk yield or poor BCS (Melendez et al., 2007; Weber et al., 2015) rather than estimated calving dates. This is particularly true for primiparae who have yet to reach their mature size (Berry et al., 2006; Coffey et al., 2006) and have a lower intake capacity as evidenced by their lower feed intake (Azizi et al., 2009). High concentrate diets may help primiparous cows to reach their potential lactation length easier than pasture alone, demonstrated by their longer lactations in confinement systems relative to older cows (M'hamdi et al., 2012; Hossein-Zadeh, 2013). Conversely, multiparous cows may be able to achieve their potential lactation length based on almost exclusively pasture. Additionally, without the emphasis on achieving a 365-d calving interval in confinement systems, primiparous cows are associated with an extended calving interval, across multiple dairy breeds (391 to 407 d; Hare et al., 2006). Conversely, in pasture-based systems, primiparous Holstein-Friesian cows were associated with shorter calving intervals (367 d; Evans et al., 2006) and, therefore, shorter lactations.

Reducing the proportion of primiparous cows in the herd could be achieved through improving the health

and fertility status of the herd, which, in turn, could contribute to longer lactations being achieved in pasture-based production systems. In addition to increased milk production from longer lactations, multiparous cows have been associated with higher standardized 305-d milk yield relative to primiparae (Horan et al., 2005; Lee and Kim, 2006). Nevertheless, reducing the proportion of primiparous cows may not be feasible in expanding herds where additional heifers are bred to fulfill expansion requirements.

The effect of shortening the dry period on lactation yield has been extensively studied (Bachman and Schairer, 2003; Rastani et al., 2005; Pezeshki et al., 2008; Atashi et al., 2013), with many suggesting shortening dry periods would improve energy balance and metabolic status in early lactation, without affecting lactation production (Rastani et al., 2005; Pezeshki et al., 2008). The traditional dry period of approximately 60 d enables the involution and regeneration of the mammary gland (Capuco et al., 1997). The results of the effect of dry period on milk production are, however, inconsistent (Rastani et al., 2005; Pezeshki et al., 2008; Atashi et al., 2013), with many reporting that shorter dry periods were associated with shorter lactations (present study) or actually lower yields in the subsequent lactation, particularly in early lactation (Pezeshki et al., 2008; Atashi et al., 2013). Conversely, Rastani et al. (2005) reported no effect on solid-corrected milk yield in 65 primiparous and multiparous US Holstein cows following dry periods of <28 d relative to a traditional-length dry period. While longer lactations before dry-off may compensate for lower yields (Pezeshki et al., 2008; Atashi et al., 2013), no study, to our knowledge, has looked at the effect of repeated short dry periods on production. Nonetheless, corroborating most previous studies in dairy cows, where dry periods of traditional lengths were associated with the highest production levels (Pezeshki et al., 2008; Atashi et al., 2013), dry periods of between 36 and 77 d were associated with the longest lactations in the present study.

Although not considered as a factor associated with lactation length in previous studies, the longer lactation and higher likelihood of achieving LL270 and LL305 associated with requiring veterinary assistance at calving in the present study were likely due to delayed submission and conception in cows that experienced a very difficult calving. Haile-Mariam et al. (2003) reported a phenotypic correlation of 0.47 between calving interval and lactation length in Australian dairy cows. Using data available from the Irish national database, Berry et al. (2019) reported that multiparous cows that required veterinary assistance at calving had a 15.1-d longer calving interval than those that required no

assistance at calving. Greater calving difficulty may lengthen lactations, as some producers dry off cows based on expected calving dates, yet the delayed calving in the subsequent lactation would likely lead to a shorter subsequent lactation or even culling.

Breed Effects

The longer average lactations in Holstein-Friesian cows relative to Montbéliarde and Norwegian Red cows detected in the present study has not been previously reported. An Irish study comparing the production efficiency of imported French dual-purpose breeds (35 Montbéliarde cows and 33 Normande cows) and 64 Holstein-Friesian cows (31 imported from Holland and 33 upgraded Irish Holstein-Friesians) reported no significant difference in lactation length between breeds in a spring-calving, pasture-based system (Dillon et al., 2003). Dillon et al. (2003) did, however, report a 5-d longer lactation in Dutch imported Holstein-Friesian relative to Montbéliarde cows, although it was not significant.

Interbreed differences in lactation persistency have been reported since the 1980s (Wood, 1980; Grossman et al., 1986). Neither lactation length nor lactation persistency are included in the genetic evaluations of the Economic Breeding Index (the Irish dairy breeding index spanning all dairy breeds; Berry et al., 2007). While Norman et al. (1985) recommended extending lactation yields of all cows dried off early to the standardized length for genetic evaluations, this could contribute to a bias in yield estimates for cows that, in particular, were dried off early (which could include cows that dried themselves off naturally). Hence, to fairly compare breeds of different persistency, consideration should be given to including lactation length in genetic evaluations or breeding objectives where cows naturally cease lactation before the standardized lactation length. Recording the reason for dry-off (e.g., natural or injury) may be useful in ensuring a differentiation is made between animals with a genetic predisposition to shorter lactations versus those that had a short lactation for some random reason not captured in a contemporary group effect (e.g., injury). How best to handle short lactations in either genetic evaluation models or breeding objectives warrants further investigation while continuing to conform to ICAR guidelines. This could involve the status quo test-day model genetic evaluation procedure and some post-hoc adjustment or scaling of yield for differences in genetic merit for lactation length. Consideration should also be given to the use of lactation length in the generation of cow-specific phenotypic yields, thus achieving closer

concordance between the sum of the lactation yields per cow and the total herd milk supplied to the processor.

Intrabreed Effects

To our knowledge, no study has reported heritability estimates for lactation length in seasonal-calving, pasture-based dairy herds with multiple European dairy breeds. The heritability estimate of lactation length in the present study was lower than previously reported in pasture-based Holstein-Friesian cows in Australia (0.03; Haile-Mariam et al., 2003) and in confinement-based cows of multiple dairy breeds (0.06 to 0.37; Ojango and Pollott, 2001; Bakir et al., 2004; Goshu et al., 2014). The repeatability estimates for lactation length reported in confined cows (0.11 to 0.65; Ojango and Pollott, 2001; Bakir et al., 2004) was higher than that reported in the present study (0.04). The coefficient of genetic variation, though not previously reported, was calculated from the documented statistics provided in other studies for Holstein-Friesian cows (Ojango and Pollott, 2001; Goshu et al., 2014). The coefficient of genetic variation for lactation length in the present study (i.e., 1.2%) was lower than that previously reported in Holstein-Friesian cows (5.3% to 15.3%; Ojango and Pollott, 2001; Goshu et al., 2014). The complexity of factors associated with lactation length in pasture-based systems, particularly the reliance on the calving pattern to coincide with commencement of grass growth (Berry et al., 2013) and maintenance of a 365-d calving interval, are reflected in the lower heritability estimate and coefficient of genetic variation of lactation length relative to those reported from confinement systems. In an analysis of 2,060,784 lactation records from 1,022,329 cows, Berry et al. (2013) reported a heritability of fertility traits varying from 0.01 to 0.07, which is consistent with the heritability of 0.01 to 0.03 for lactation length in the present study. This was also reflected in the lower heritability estimates for lactation length in cows calving in March (0.018) or April and May (0.013) relative to cows calving in January (0.025) or February (0.024), echoing the seasonal nature of Irish dairy production. As cows are generally dried off over a strict period in early winter, cows calving in January or February have the necessary time to reach their potential lactation length and will likely only be dried off early when milk yield is low. Although the heritability estimates of lactation length in January and February are likely to somewhat reflect the heritability of yield in late lactation (0.16 to 0.27; Bastin et al., 2011; McCarthy and Veerkamp, 2012), the lower heritability estimate of lactation length relative to late lactation milk yield is likely due to the influence of other management factors or decisions.

Conversely, the length of lactation of March-, April-, or May-calving cows is more reflective of the low heritability of fertility traits (Berry et al., 2014). The greater influence of management factors in later-calving cows is reflected in the higher coefficient of residual variation in April- and May-calving cows (0.11) relative to those calving in January (0.07).

Genetic gain is a function of selection intensity, accuracy of selection, genetic standard deviation, and generation interval (Rendel and Robertson, 1950). Selection accuracy is the only component directly influenced by heritability. Nonetheless, the same selection accuracy can be achieved irrespective of heritability once sufficient data are available (Berry et al., 2011). Hence, if dry-off dates and reason for drying off were frequently recorded, as could be the case if recording was mandatory, high selection accuracy for lactation length could be achieved. Of importance then would be the extent of the genetic variability. Based on the genetic standard deviation estimated in the present study (3.3 d), the top 20% of cows on genetic merit for lactation length would be expected, on average, to have a 9.2-d longer lactation than cows in the bottom 20%. This difference increased to 11.6 d when the top and bottom 10% of cows were compared. Similarly, when based on the estimated genetic variability for LL305, the top 20% of cows genetically would be, on average, 8.1 percentage units more likely to achieve lactations of 305 d or longer than the bottom 20% of cows. This difference increases to 10 percentage units when the top and bottom 10% are compared.

Poor fertility often results in longer calving intervals and therefore longer lactations in year-round calving systems (Tiezzi et al., 2012). In seasonal-calving, pasture-based systems, however, where cows tend to be dried off on a given date, poor fertility leading to delayed calving dates actually results in shorter lactations. Increasing the proportion of cows that calve early in the calving season, achieved through improved fertility, should result in longer lactations. Hence, the improvements in the genetic merit for lactation length of Holstein-Friesian cows and sires achieved to date are likely due to the year on year improvement in genetic merit for reproductive performance in Irish dairy cows (Berry et al., 2014). Both the genetic variation in lactation length and the improvements in genetic merit for lactation length already achieved highlight the considerable progress achievable through breeding.

CONCLUSIONS

With only 27% of the cows in the present study achieving lactations of 305 d or greater, the suitability

of yields standardized to a 305-d lactation, without the consideration of lactation length or persistency for genetic evaluations and decision support tools, is questionable. While the heritability estimates for lactation length in the present study were lower than previously reported (for cows in confinement production systems), genetic variation exists for lactation length in pasture-based dairy cows. Given the array of genetic and nongenetic factors associated with lactation length, an approach combining selective breeding and improvements in management practices may prove an efficient and effective strategy to lengthen lactations.

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