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Validation of a beef cattle maternal breeding objective based on a cross-sectional analysis of a large national cattle database

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Abstract

Despite the importance of validating any technology prior to recommendation for use, few studies exist in the scientific literature which have demonstrated the superior performance of high-ranking animals in a given total merit index; this is especially true for maternal cattle selection indexes. The objective of the present study was to demonstrate the impact of the Irish total merit maternal-based index and provide the benefits of using the Irish total merit maternal-based beef index as part of a breeding policy. The validation exercise was undertaken using 269,407 records (which included the cow's own records and her progeny records) from 92,300 females differing in a total merit index for maternal value; a comparison was also made with the Irish terminal index. Association analyses were undertaken within the framework of linear and threshold mixed models; the traits analyzed were fertility (e.g., calving interval), slaughter (e.g., harvest weight), live weight (e.g., weaning weight), and producer-recorded traits (e.g., docility). All traits were analyzed with the maternal index and terminal index fitted as covariate(s) separately. Depending on the independent variable analyzed, the other fixed effects included: parity of cow, heterosis and recombination loss of cow and/or progeny, gender of progeny, and the estimated breeding value of the sire; contemporary group was included as a random effect. The results demonstrate the effectiveness of using total merit indexes to improve performance in a whole range of different traits, despite the often antagonistic genetic correlations among traits that underpin the index. Cows excelling on the maternal index had less calving difficulty, superior fertility performance, lighter carcasses, and live weight, as well as being more easily managed. Additionally, progeny of higher maternal index cows were lighter at birth and more docile albeit with a small impact on slaughter traits. In contrast, higher terminal index cows had more calving difficulty, compromised fertility and had heavier carcasses themselves as well as their progeny. While the differences in phenotypic performance between groups on maternal index was, in most instances, relatively small, the benefits are: (1) expected to be greater when more genetically extreme groups of animals are evaluated and (2) expected to accumulate over time given the cumulative and permanent properties of breeding schemes.

Key words: beef, carcass, fertility, genetic, index, phenotypic

Introduction

The major challenges facing modern-day beef production include its relatively large contribution to global greenhouse gas emissions (54% of total livestock greenhouse gas

emissions; Caro et al., 2014) as well as its relatively poor economic return for producers (Hocquette et al., 2018). Genetic improvement in the beef sector, especially of the cow herd, will be key to the sustainability of beef production via a

Abbreviations	
CG	contemporary group
CR42	calving in the first 42 d of the herd
	calving period
EBV	estimated breeding value
EUROP	European Union beef carcass
	classification system
ICRE	Irish Cattle Breeding Federation

reduction in carbon footprint (Fennessy et al., 2018; Quinton et al., 2018) concurrent with sustaining or improving herd profitability (MacNeil, 2016).

Breeding indexes in beef cattle generally represent either (1) terminal breeding indexes designed to identify the most profitable parents of animals intended for slaughter or (2) maternal breeding indexes designed to identify the most profitable parents of animals destined to become dams of the next generation. Both Amer et al. (1998) and Connolly et al. (2016) described terminal beef indexes for the UK and Ireland, respectively. Connolly et al. (2016) proceeded to validate the terminal index using actual performance data of animals from the Irish national database stratified on their terminal index at birth. Maternal breeding indexes in cattle are not often described in the scientific literature although Roughsedge et al. (2005) and Ochsner et al. (2017) outlined a maternal beef breeding index for the UK and USA, respectively. Using a relatively small controlled study of 82 beef cows divergent on the Irish national maternal index, McCabe et al. (2019) failed to detect a significant difference between the high maternal index group (n = 41) and the low maternal index group (n = 41) for body weight, body condition score, milk yield, and a range of feed intake traits. McHugh et al. (2014) evaluated the phenotypic performance of 38,619 beef cattle differing in genetic merit for individual fertility, calving performance, and weaning weight traits. Although the observed phenotypic differences sometimes deviated from expectations based on genetic merit, the sign of the association between the phenotype and estimated breeding value (EBV) for that trait was in line with expectation (McHugh et al., 2014). The literature is, however, void of a study which has attempted to validate a maternal index in beef cattle using any crosssectional analysis of a large dataset.

Quantifying the mean performance of both progeny and cows differing on maternal index value is crucial to instill confidence among breeders and producers alike as to the benefits of multitrait selection using an index. This is particularly important given the known genetic antagonisms that exist between terminal traits and maternal traits (Roughsedge et al., 2005; Berry and Evans, 2014) and thus the potential unease that may exist concerning the impact selection nationally on a maternal index could have on terminal characteristics (e.g., carcass yield and quality). The objective, therefore, of the present study was to evaluate the phenotypic differences for a range of economically important traits in the progeny, as well as beef cows themselves, differing in genetic merit for the Irish maternal breeding index. Results would be important in validating a national maternal index, as well as demonstrating to stakeholders the actual phenotypic benefit of adopting an index approach to improving cow maternal characteristics and the impact on the terminal characteristics of the resulting progeny.

Materials and Methods

Ancestry and breed composition (i.e., estimated using pedigree) information, weight records, reproductive performance records (i.e., service dates, pregnancy diagnoses, and calving dates), producer-recorded traits (i.e., calving difficulty, calf quality, calf and cow docility, and milk scores) as well as carcass-related information (i.e., carcass weight, conformation, and fat score) were available from the national database managed by the Irish Cattle Breeding Federation (ICBF) on individual animals. EBVs from historical national genetic evaluations were also available.

Genetic trends

EBVs were extracted from the April 2019 Irish domestic genetic evaluations for all females that had at least 1 calving event. To ensure that only beef cows were retained, only females with a known sire and where dairy breed composition was ≤55% were retained. Mean annual values by year of first calving for the Irish terminal and maternal indexes, as well as EBVs for individual component traits of both indexes were calculated. Genetic gain in each trait was expressed in genetic standard deviation (SD) units relative to the year 2000 (Supplematary Table 1).

Validation population

A validation population of females was generated for quantifying the association between female genetic merit assigned at birth with subsequent phenotypic performance of the female herself and her direct progeny. Females born in the years 2012 and 2013, which had at least 1 subsequent calving event, were retained for use in the validation population. Only females where ≤55% of their breed composition was dairy bloodlines were retained as were those with a known sire. EBVs for a series of traits from the December 2013 Irish domestic genetic evaluations were used in the validation process. The ICBF, who are responsible for the national beef genetic evaluations in Ireland, undertake routine multibreed genetic evaluations for each of the suites of traits: carcass, calving performance, docility, milk ability, and cow fertility. All evaluations are based on a multibreed population and are undertaken in a multitrait framework using the MIX99 software suite (Lidauer et al., 2011). The majority of Irish beef cattle are crossbred and hence all evaluations adjust for the heterosis and recombination loss coefficient of the animal. The use of genetic groups in the genetic evaluation accounts for breed differences. Further details on the ICBF genetic evaluations are in the study Evans et al. (2007, 2009). The maternal and terminal index for each animal was computed for all animals using index weightings for the Irish national maternal and terminal index, described in Supplementary Table 1, and which reflect those that have been used in Ireland since 2016. The maternal index of each female was also divided into 5 groups with approximately in equal number of animals in each: very high (≥ €260), high (≥ €210 and < €260), average (≥ €160 and < €210), low (≥ €110 and < €160), and very low (< €110).

Reproductive performance traits

Data were available between the years of 2014 and 2018, inclusive, on 4,679,401 calving records from 1,705,920 beef cows. Fertility phenotypes were defined similar to those described in detail by Berry and Evans (2014) for the Irish national beef cow genetic evaluation. Age at first calving was defined as the age, in days, when the heifer calved for the first time; only records between 660 and 1400 d of age were retained. Calving interval was defined as the number of days between consecutive calving events; only calving interval records between 300 and 800 d were retained as per the national genetic evaluation (Berry and

Seasonal calving predominates in Ireland (Berry and Evans, 2014); Irish beef cows are generally bred and calve within a time period. The calving period in the present study was defined separately for primiparae and multiparae. The start date of the calving period for a herd was the first calendar date which was followed by ≥5 calving events within the subsequent 14 d; the end date of a calving period was the last calving date which was not followed by a subsequent calving in that herd anytime in the following 21 d. Only calving periods between 35 and 200 d in length were retained. Calving periods, and the traits defined from these, for primiparous and multiparous cows with <6 or <20 calving records, respectively, were not considered further. Calving in the first 42 d of the herd calving period (CR42) was defined per cow as a binary trait, based on whether or not a cow calved in the first 42 d of the defined calving period; cows were not considered if they did not calve any time during the defined calving season.

Cow survival was defined as whether or not a cow successfully reached the next lactation. A cow was deemed to have survived lactation n if she had a subsequent calving date for lactation n + 1 within 800 d of her calving date for lactation n. A cow that did not have a calving date for lactation n + 1 and was recorded to have either been slaughtered or died, was deemed to have not survived lactation n. Cow survival was only defined for lactations ≤5. There were 3,833,598 lactation records from 1,405,230 cows with at least 1 fertility trait remaining.

Live weight

A total of 2,310,170 live weight records, captured on-farm between January 2014 and June 2019, inclusive, were available for the present study. Live weight records were divided into 3 different categories based on the age of the animal when weighed.

Birth weight

Birth weight was defined as the live weight record, measured using a weighing scale, in the first 14 d of life. Only the earliest weight record was retained per animal. Birth weight records <20 or >100 kg were discarded; 44,136 birth weight records from 1,431 herds remained.

Weaning weight

Weaning weight was defined as the live weight recorded, on-farm, between 120 and 350 d of age, inclusive. Only weaning weight records between 100 and 650 kg were considered further and only the weight recorded closest to 200 d of age was retained; a total of 452,280 weaning weight records were available.

Cow weight

Live-weight records of females that had been recorded to have already calved were defined as cow weight. Cow live weights recorded >350 d after their last calving date were not considered further. Only 1 weight per lactation was considered which was the weight recorded closest to 200 d postcalving. A total of 129,798 cow live weight records from 116,176 cows remained for further analysis.

Producer-recorded traits

Traits recorded by producers between January 2014 and June 2019, inclusive, were also available to the present study and included calving difficulty (n = 4,057,100), calf quality (n = 2,956,909), calf

docility (n = 2,956,909), cow docility (n = 3,025,355), and cow milk scores (n = 3,020,027).

Calving difficulty

Calving difficulty is subjectively scored by Irish producers on a linear scale of 1 to 4 at calving, where 1=no calving assistance, 2=slight assistance, 3=considerable assistance and 4=veterinary assistance. Data from herd-years where >95% of animals were recorded as having the same calving difficulty score were removed; 2,403,016 calving difficulty records from 1,044,704 cows were retained. For the purpose of the present study, calving difficulty scores were collapsed into a binary trait, calving dystocia (score 1 and 2 combined vs. 3 and 4 combined).

Calf quality

Calf quality is subjectively scored by Irish producers on a 5-point linear scale based on thrive and conformation of the calf at weaning: 1 = very poor quality, 2 = poor quality, 3 = average quality, 4 = good quality, and 5 = very good quality. Calf quality scores from herd-years where >95% of animals were recorded as having the same calf quality score were removed. A total of 1,812,053 scores recorded on animals aged between 120 and 360 d and recorded in the herd they were born in were retained.

Calf and cow docility

Calves are subjectively scored by Irish producers at weaning on a scale of 1 (docile) to 5 (aggressive). For the purposes of this study, the scale was reversed to be consistent with that undertaken for Ireland's genetic evaluation. Calf docility scores from herd-years where >95% of the calves were recorded as having the same calf docility score were not considered further. Furthermore, only calf docility scores recorded on animals aged between 120 and 360 d and recorded in the herd of birth were retained. Cows are subjectively scored by Irish producers at weaning on a scale of 1 (aggressive) to 5 (docile). Cow docility score data from herd-years where >95% of cows were recorded as having the same cow docility score were discarded. Only cow docility scores recorded in the first 350 d postcalving and recorded in the herd that the calving event occurred in were retained. A total of 1,812,053 calf docility records and 2,138,163 cow docility records from 959,230 cows remained.

Milk scores

Cow milk scores were subjectively scored by Irish producers for each lactation on a 5-point linear scale; 1 (poor milk ability) to 5 (good milk ability). Cow milk scores from herd-years where >95% of cows were recorded as having the same milk score were removed. Only milk scores recorded on cows <350 d calved and recorded in the herd of the most recent calving event were retained; 2,135,519 records from 958,094 cows remained.

Carcass data

Carcass weight (kg), conformation score (scale: 1 to 15; Englishby et al., 2016), and fat score (scale: 1 to 15; Englishby et al., 2016) were available for 8,658,722 animals slaughtered from January 2014 to June 2019. Carcass weight was measured, on average, 1 h after slaughter following the removal of the head, legs, thoracic and abdominal organs, and internal fats and hide. As described by Pabiou et al. (2011), carcass conformation and fat scores were graded using video image analysis and were graded under the European Union beef carcass classification system (EUROP). The resulting EUROP classification grades were transformed into a 1 to 15 scale as outlined by Englishby et al. (2016). This 15-point conformation classification system attempts to describe the

conformation of the animal mainly based on the round, back, and shoulder; a score of 1 reflects poor conformation while that of 15 reflects excellent conformation (Englishby et al., 2016). Carcass fat score attempts to describe the fat cover on the outside of the carcass and in the thoracic cavity and is graded from 1 (low fat cover) to 15 (high fat cover; Englishby et al., 2016).

Carcass data were stratified into: (1) young animals that had never parented an animal and (2) cows. For the young animal category, heifers and steers slaughtered between 14 and 36 mo of age, and young bulls slaughtered between 12 and 24 mo of age were retained. Carcass records for cows were those from females harvested between 24 and 426 mo of age with at least 1 calving record. Carcass records from cows slaughter >24 mo since their last calving date were not considered further. Furthermore, carcass records were discarded from all animals that resided in >3 herds during their lifetime, and/or were present in the herd they were slaughtered from <100 d prior to slaughter. There were 1,814,301 young animal and 904,772 cow carcass records remaining, respectively, after edits.

Contemporary groups

Only slaughter, producer-recorded, fertility, and weight traits from validation cows and their direct progeny were retained. Progeny of the validation cows were not considered further if the sire of the progeny had not been recorded. The EBVs from the April 2019 Irish domestic genetic evaluations for the sire of the progeny were available for use in the statistical models (described later).

Herd-year-season contemporary groups (CG) were generated for each trait separately for the validation cows (and their progeny) using an algorithm described in detail by Berry and Evans (2014). This algorithm creates CGs based on activity events (e.g., calving, slaughter, and weight recording) from herd contemporaries occurring in close proximity. For the present study, fertility (except age at first calving) traits, calving difficulty traits, milk score, cow docility score, and cow weight traits were grouped based on a combination of both calving date and herd of calving. Birth weight, weaning weight, calf docility score, and calf quality score of the progeny were grouped based on their date and herd of birth. CG for age at first calving was based on the calving date and the herd the animal resided in 9 mo prior to calving. Slaughter traits (i.e., carcass weight, conformation, and fat) for cows and young animals were grouped based on date of slaughter, herd prior to slaughter, and gender (i.e., heifer, steer, and young bull). For age at slaughter in young animals, animals were grouped based on gender, the herd at slaughter, and the date they entered that herd. An additional CG was also created for the weight and slaughter traits, which was herd-date of weighing or abattoir-date of slaughter, respectively. CGs with <3 animals were not considered further. The final dataset consisted of 178,395 lactation records with at least 1 fertility trait, 188,790 lactation records with at least 1 producer-recorded trait for either the cow or her progeny, and 16,808 lactation records with at least 1 live weight for either the cow or her progeny, as well as 28,480 slaughter records for cows (n = 1,150) or young animals (n = 27,330; Table 1).

Data analysis

The association of the maternal and terminal index with the quantitative phenotypic performance traits was quantified using linear mixed models in ASREML (Gilmour et al., 2009). For the binary traits, threshold models were used with a logit-link function in ASReml (Gilmour et al., 2009), assuming a binomial distribution of the residuals. For all models, the maternal index was considered either on a continuous scale or on a categorical scale (i.e., very high, high, average, low, and very low); the terminal index was considered on a continuous scale for all traits. The association between each phenotypic

Table 1. Number of cows, records, and contemporary group (CG), as well as the mean (µ) and SD for each trait

Trait	Cows	Records	CG	μ	SD
Weight traits					
Progeny birth weight (kg)	2,512	3,315	900	44.00	8.00
Progeny weaning weight (kg)	8,480	13,523	2,652	291.00	75.00
Cow live weight (kg)	2,909	3,361	705	677.00	98.00
Fertility traits					
Age at first calving (d)	47,699	47,699	10,413	945.00	156.00
Calving interval (d)	56,372	130,887	28,572	389.00	71.00
Cow survival (1/0)	67,951	161,031	33,163	0.87	0.33
Calving in first 42 d (1/0)	15,934	26,692	4,821	0.71	0.46
Carcass traits					
Progeny carcass weight (kg)	21,475	27,330	5,781	377.00	56.00
Progeny carcass conformation (1 to 15)1	21,475	27,330	5,781	9.54	1.70
Progeny carcass fat (1 to 15)1	21,475	27,330	5,781	7.90	2.10
Progeny age at slaughter (d)	21,475	27,330	5,781	713.00	152.00
Cow carcass weight (kg)	1,150	1,150	350	381.00	59.00
Cow carcass conformation (1 to 15)1	1,150	1,150	350	7.90	1.90
Cow carcass fat (1 to 15)1	1,150	1,150	350	9.40	2.60
Producer recorded traits					
Cow docility score (1 to 5) ²	46,449	103,453	20,549	4.07	0.79
Cow milk score (1 to 5) ²	46,444	103,361	20,533	3.90	0.79
Calving difficulty (%)	68,191	183,984	38,119	0.17	0.37
Dystocia (%)	68,191	183,984	38,119	0.04	0.19
Progeny docility score (1 to 5) ²	40,473	82,670	16,381	2.00	0.75
Progeny quality score (1 to 5) ²	40,473	82,670	16,381	4.12	0.74

Scale of 1 (poor conformation /little fat cover) to 15 (excellent conformation/heavy fat cover).

²Scale of 1 (aggressive/poor milk ability/very poor quality) to 5 (docile/good milk ability/very good quality).

performance trait and its respective EBV was also quantified in a separate series of analyses. The models for the cow fertility traits were:

$$\begin{aligned} A &= Index + Het_{cow} + Rec_{cow} + age_{calving} X parity \\ &+ gender + HYS_{calving} + cow + e \end{aligned}$$

$$B = Index + Het_{cow} + Rec_{cow} + HYS_{insem} + e$$

$$\begin{aligned} \text{Logit} \left\{ P \left(C = 1 \mid X \right) \right\} &= \text{Index} + \text{Het}_{\text{cow}} + \text{Rec}_{\text{cow}} + \text{age}_{\text{calving}} X \text{parity} \\ &+ \text{gender} + \text{HYS}_{\text{calving}} + \text{cow} + \epsilon \end{aligned}$$

where A is the dependent variable for calving interval; B is the dependent variable for age at first calving; $Logit\{P(C = 1|X)\}\)$ is the logit of the odds of a positive outcome for CR42 or cow survival; Index is the fixed covariate or factor representing either the maternal index or terminal index (as either a class or a continuous variable); Het com is the fixed factor of a general heterosis coefficient of the cow (i.e., 0.0, 0.01 to 0.10, 0.11 to 0.2, ..., 0.91 to 0.99, 1.0); Rec____ is the fixed class effect of a general recombination loss coefficient (i.e., 0.00, 0.001 to 0.050, 0.051 to 0.100, ..., 0.451 to 0.499, 0.500, > 0.500); parity is the fixed factor of parity (i.e., 1, 2, 3, 4, 5+); age_{calving} is the fixed effect factor of age at calving in months relative to the median age of the parity; gender is the fixed factor of gender of the calf; ${\ensuremath{\mathsf{HYS}}}_{\ensuremath{\mathsf{calving}}}$ is the random factor of herd-year-season of calving; HYS is the random factor of herd-year-season of insemination; cow is the random factor of the cow, where Cow $\sim N(0, I\sigma_{cow}^2)$ with σ_{cow}^2 representing the cow variance and I the identity matrix, and e is the random residual factor, where $e \sim N(0, I\sigma_e^2)$ with σ_e^2 representing the residual variance.

The models fitted to the weight traits were:

$$\begin{split} D &= Index + Het_{cow} + Rec_{cow} + age_{calving} Xparity \\ &+ DSC + HYS_{calving} + herd_date + cow + e \end{split}$$

$$\begin{split} E &= Index + Het_{cow} + Rec_{cow} + Het_{calf} + Rec_{calf} \\ &+ age_{calving} Xparity + age\ Xgender + sire_{cd} \\ &+ HYS_{birth} + herd_date + cow + \ e \end{split}$$

$$\begin{split} F &= Index + Het_{cow} + Rec_{cow} + Het_{calf} \\ &+ Rec_{calf} + age_{calving} \ Xparity \\ &+ age \ Xgender + EBV_{dwwt} + HYS_{birth} \\ &+ herd \ date + cow + e \end{split}$$

where D is the dependent variable for cow weight; E is the dependent variable for birth weight; F is the dependent variable for weaning weight; DSC is the fixed factor of number of months since date of calving; $\operatorname{Het}_{\text{\tiny calf}}$ is the fixed factor of a general heterosis coefficient of the calf; Rec_{calf} is the fixed factor of a general recombination loss coefficient of the calf; age is the fixed covariate of calf age in days; sire cd is the fixed covariate of EBV for direct calving difficulty of the calf's sire; EBV dwwt is the fixed covariate of EBV for direct weaning weight of the calf; HYS, is the random factor of herd-year-season of birth and herd_date is the random factor of herd-date of weighing.

The models for the producer-recorded traits were

$$\begin{split} G &= Index + Het_{cow} + Rec_{cow} + Het_{calf} + Rec_{calf} \\ &+ age_{calving} \; Xparity + gender + age_{mo} + sire_{cwt} \\ &+ sire_{conf} + HYS_{calving} + cow + e \end{split}$$

```
H = Index + Het_{cow} + Rec_{cow} + Het_{calf}
                  +Rec<sub>calf</sub> + age<sub>calving</sub> Xparity + age<sub>mo</sub>
                  +gender + sire<sub>doc</sub> + HYS<sub>birth</sub> + cow + e
        I = Index + Het_{cow} + Rec_{cow} + age_{calving} Xparity
              + DSC + HYS_{calving} + cow + e
Logit \{P(J = 1|X)\} = Index + Het_{cow} + Rec_{cow} + Het_{calf}
                             +Rec_{calf} + age_{calving} + parity + gender
                             +sire_{cd} + HYS_{calving} + cow + e
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where G is the dependent variable for cow milk score or calf quality score; H is the dependent variable for calf docility score; I is the dependent variable for cow docility score; Logit{P(J = 1|X)} is the log of odds of a positive outcome for dystocia; age_{mo} is the fixed factor of the age of calf in months; sire cut is the fixed covariate of EBV for carcass weight of the calf's sire; sire, is the fixed covariate of EBV for carcass conformation score of the calf's sire and sire doc is the fixed covariate of EBV for the docility of the calf's sire.

The models for the carcass traits were

$$K = Index + Het_{cow} + Rec_{cow} + age_{calving}$$

+ parity + DSC + HYS_{slau} + e

$$\begin{split} L &= Index + Het_{cow} + Rec_{cow} + Het_{calf} \\ &+ Rec_{calf} + age_{calving} + parity + type \quad Xage_{mo} \\ &+ sire_{depvar} + HYS_{slau} + abbatoir_date + cow + e \end{split}$$

$$\begin{split} M &= Index \ + Het_{cow} + Rec_{cow} + Het_{calf} + Rec_{calf} \\ &+ age_{calving} Xparity + sire_{cwt} + carcass_{cwt} \\ &+ carcass_{fat} + HYS_{slau} \ + e \end{split}$$

where K is the dependent variable for carcass weight, conformation, or fat of the cow herself; L is the dependent variable for progeny carcass weight, conformation, or fat score; M is the dependent variable for age of slaughter; type is the fixed factor for gender of slaughter animal (i.e., heifer, steer, and young bull); $\operatorname{sire}_{\text{\tiny depvar}}$ is the fixed covariate of the EBV for the dependent variable of the calf's sire; $\mathsf{carcass}_\mathsf{cwt}$ is the fixed covariate for actual carcass weight of the animal; carcass fat is the fixed covariate for actual carcass fat of the animal; HYS_{slau} is the random factor of herd-year-season of slaughter date and abbatoir_date is the random factor of abattoir date of slaughter.

Secondary analyses were undertaken using the same models as described above except that index was replaced with the EBV corresponding to the dependent variable under investigation. While the indexes and EBVs used in the present study from the national genetic evaluations are across breed, it was also of interest as to whether the expected change in performance was due to a breed substitution effect or a within breed effect or both. To investigate this, a separate series of analyses were carried out in which individual breed covariates (i.e., Aberdeen Angus, Holstein/Friesian, Limousin, Hereford, Belgian Blue, Charolais, Simmental, Aubrac, Parthenaise, and other breeds) were also included in all models as fixed effects. The representation of each breed in the dataset of cows is in Figure 1.

For the binary traits, the probability of the event occurring per unit increase in the indexes and corresponding EBV was estimated using the model solutions from the multiple regression analyses. Odds ratios were calculated as the exponent of the model solutions. To compare phenotypic performance of the maternal index groups, least squares means for each trait analyzed for each of the maternal index groups were extracted based on a referent animal and a linear function of the model solutions. A referent animal was chosen for each trait to compare to common animal.

Results

Genetic trends

The genetic SD of each of the traits EBVs are presented in Supplementary Table 1. Little genetic gain (0.13 SD units in total) has occurred in the Irish terminal index of beef breeding females since 2000 (Figure 2). Total genetic gain in the maternal index was 0.21 SD units from 2000 to 2013, with

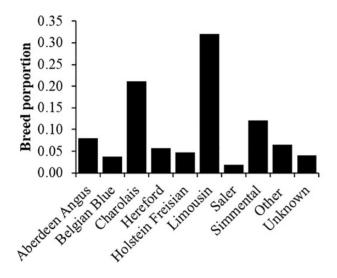


Figure 1. Mean breed composition of cows in dataset.

a further 0.38 SD units from 2013 to 2018 (Figure 2). Genetic merit for maternal calving difficulty has improved steadily since 2004. In contrast, genetic merit for direct calving difficulty deteriorated (i.e., increased calving difficulty) by 0.34 SD units from 2000 to 2015, but improved (i.e., reducing calving difficulty) by a total of 0.07 SD units from 2015 to 2018 (Figure 3). Erratic genetic trends were evident for both gestation length and calf mortality at birth in the early years but, since 2000, both traits have improved by a total of 0.30 and 0.17 SD units, respectively. Since 2000, genetic merit for age at first calving has improved (i.e., decreased) by 0.52 SD units while genetic merit for cow survival has increased by 0.68 SD units (Figure 3). Between 2000 and 2014, genetic merit for calving interval has increased by 0.41 SD units, but between 2015 and 2018 calving interval improved (i.e., decreased) by a total of 0.16 SD units. From 2003 to 2018, carcasses became genetically heavier and leaner (Figure 4). Genetic trend for conformation score has been inconsistent, with the genetic merit of progeny from first calving cows in 2018 remaining stable since 2000 (Figure 3). Genetic trends for both carcass weight and live weight of cows were similar from 2000 to 2012 (Figure 4). From 2012 to 2018, genetic merit for live weight of cows increased by 0.27 SD units while cow carcass weight increased by 0.07 SD units. Maternal weaning weight and docility score were 0.37 and 0.41 SD units higher, respectively, in 2018 than they were in 2000.

Associations with reproductive performance

When fitted as a linear covariate, superior maternal index values were associated with an improvement (P < 0.05) in all reproductive traits evaluated. Each SD unit improvement in the maternal index was associated with a reduction by 4.08 and 0.89 d in age at first calving and calving interval, respectively, while the odds ratio for cow survival and calving rate in 42 d were 1.11 and 1.05 greater, respectively (Table 2). The regression coefficients of the reproductive traits on the maternal index were similar irrespective of whether or not breed covariates were included in the model, suggesting that the expected improvements were not simply due to a breed substitution effect (Table 2). When stratified into 5 groups on maternal index, cows in the very high maternal group had superior reproductive performance for all 4 fertility traits analyzed

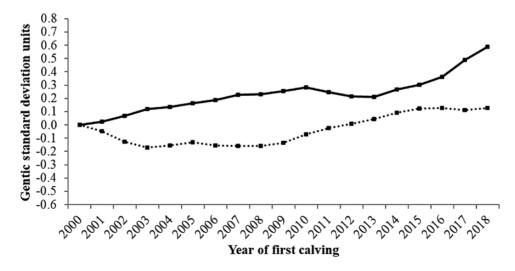


Figure 2. Genetic change, in genetic SD units of estimated breeding value (EBV), for replacement (solid black line) and terminal (dotted black line) indexes by year of first calving for females since 2000; the genetic SDs for maternal and terminal indexes were €76 and €74, respectively, both of which are based on EBV.

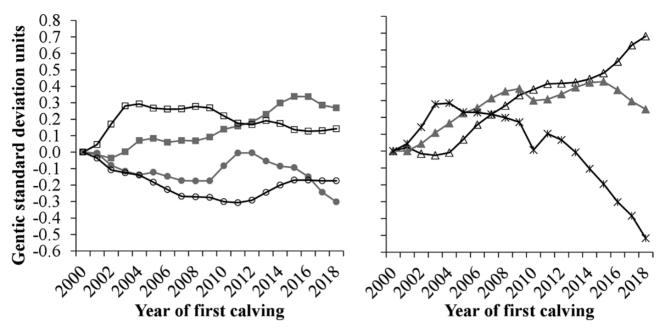


Figure 3. Genetic change, in genetic SD units (in parentheses), of the estimated breeding value for direct calving difficulty (filled squares; 6.74%), maternal calving difficulty (open squares; 5.08%), gestation length (filled circles; 5.72 d), calf mortality at birth (open circles; 1.86 units), age at first calving (asterisks; 42.8 d), calving interval (filled triangles; 6.6 d), and cow survival (open triangles; 4.48%) by year of first calving for females since 2000.

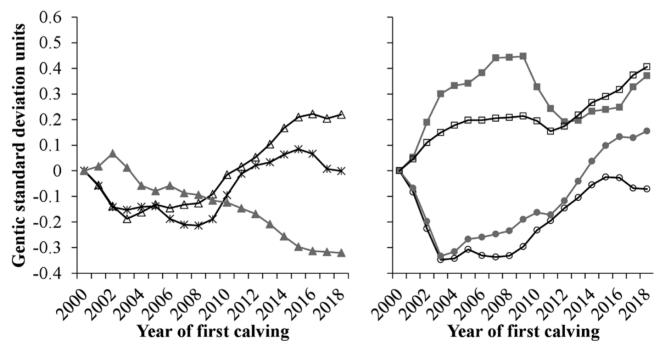


Figure 4. Genetic change, in genetic SD units (in parentheses), of the estimated breeding value for maternal weaning weight (filled squares; 22.2 kg), docility (open squares; 0.15 units), cow live weight (filled circles; 73.4 kg), cow carcass weight (open circles; 56.6 kg), progeny carcass conformation (asterisks; 2.50 units), progeny carcass fat score (filled triangles; 1.32 units), and progeny carcass weight (open triangles; 39.6 kg) by year of first calving for females since 2000.

compared to cows in the very low maternal group (P < 0.05; Table 3).

A larger terminal index value was adversely associated with reproduction (Table 2) but, once breed was adjusted for in the model, the terminal index had a favorable association with age at first calving and no association with calving interval (Table 2).

Age at first calving and calving interval increased linearly by 0.19 (0.031) days and 0.68 (0.053) days per 1 day increase in the respective EBV of the cow; the expectation was 1. The logit of the odds of a cow surviving to the next lactation increased linearly by 0.06 (SE = 0.004) per unit increase in EBV for cow survival (Table 2).

Table 2. The phenotypic change (SE) in each fertility and producer-recorded trait per SD unit change in the Maternal or Terminal index, as well as for a 1 unit change in estimated breeding value (EBV) of the respective trait, when adjusted or not for breed differences; also included is the P-value comparing the regression coefficients with or without breed adjustment

		Maternal			Terminal			EBV	
	No breed adjustment	Breed adjustment	P-value	No breed adjustment	Breed adjustment	P-value	No breed adjustment¹	${\tt Breed} \\ {\tt adjustment}^1$	P-value
Fertility									
Age at first calving (d)	-4.08 (0.61)***	-4.08 (0.61)***	66.0	8.81 (1.053)***	-6.83 (1.549)***	<0.001	0.19 (0.031)***	0.14 (0.034)***	0.262
Calving interval (d)	0.89 (0.19)***	-0.92 (0.25)***	0.91	2.10 (0.308)***	-0.05 (0.494)	<0.001	0.68 (0.053)***	0.49 (0.072)***	0.029
Cow survival $(1/0)^2$	0.10 (0.01)""	0.08 (0.01)***	0.08	-0.13 (0.012)***	-0.10 (0.020)***	0.212	0.06 (0.004)***	0.05 (0.006)***	0.462
Calving in first 42 d $(1/0)^2$	0.05 (0.02)**	0.05 (0.02)**	0.85	-0.03 (0.029)	-0.03 (0.045)	0.995	Ι	Ι	
Producer recorded traits									
Dystocia $(1/0)^2$	-0.107 (0.013)***	-0.105 (0.017)***	0.93	0.041 (0.022)	-0.023 (0.034)	0.109	0.050 (0.004)3""	0.070 (0.005)3***	<0.001
							0.058 (0.005)4***	0.068 (0.007)4***	0.245
Calf quality $(1 \text{ to } 5)^5$	0.013 (0.003)***	0.017 (0.003)***	0.31	0.022 (0.005)***	0.050 (0.007)***	<0.001	I		
Calf docility (1 to 5) ⁵	0.004 (0.002)	0.010 (0.003)***	0.12	0.006 (0.004)	0.020 (0.006)"	<0.001	0.169 (0.015)***	0.130 (0.016)***	0.105
Cow docility $(1 \text{ to } 5)^5$	0.010 (0.003)"	0.031 (0.004)""	<0.001	-0.033 (0.005)***	0.020 (0.007)"	<0.001	0.460 (0.017)***	0.379 (0.019)**	0.001
Milk score $(1 \text{ to } 5)^5$	0.077 (0.003)***	0.059 (0.003)***	<0.001	-0.095 (0.005)**	0.005 (0.007)	<0.001	I	I	

Significance of association ""P < 0.001, "P < 0.01, " * P < 0.05. ¹Missing values where trait EBVs were not available.

Walues are the loge of the odds ratio.

³Direct EBV for calving difficulty. ⁴Maternal EBV for calving difficulty. ⁵Scale of 1 (aggressive/poor milk ability/very poor quality) to 5 (docile/good milk ability/very good quality).

Table 3. Mean maternal index (Mat Index) for the 5 groups of maternal index along with the associated mean estimated breeding value (EBV) for age at first calving, calving, interval and cow survival, and the associated least square means (SE) for each of the fertility traits examined

	EE	EBV			Pheno	henotypic	
Mat Index (€)	Age at first calving (d)	Calving interval (d)	Cow survival (%)		Calving interval $(d)^2$	Cow survival $(\%)^2$	Age at first calving $(d)^3$ Calving interval $(d)^2$ Cow survival $(\%)^2$ Calving in first 42 d $(\%)^2$
99	-17.36	0.58	-0.78	990 (1.82) ^a	391 (0.52) ^a	83 (0.002)ª	75 (0.01) ^a
136	-13.64	-1.02	0.68	985 (1.64) ^b	$390 (0.45)^{ab}$	84 (0.002) ^b	74 (0.01) ^{ab}
184	-14.14	-1.70	1.66	986 (1.40) ^b	390 (0.38)ab	85 (0.002)°	75 (0.01) ^{ab}
232	-17.90	-2.68	2.46	986 (1.51) ^b	389 (0.41) ^b	86 (0.002) ^d	76 (0.01) ^{ac}
306	-26.20	4.80	3.34	977 (1.68)°	389 (0.45) ^b	87 (0.002)€	77 (0.01)°

'Referent animal had no heterosis and no recombination loss.

 $^{^2}$ Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss. 2 -Values within columns with different superscripts differ (P < 0.05) from each other.

Associations with producer-recorded traits

Calving dystocia declined with increasing maternal index of cows (Table 2). Each SD unit improvement in maternal index was associated with an improvement in calf quality (0.013 units), calf docility (0.004 units), cow docility (0.010 units), and milk score (0.077 units; Table 2). The association between maternal index and both cow docility and milk score was dependent on whether or not breed covariates were included in the model; the sign of the association, however, remained the same irrespective (Table 2). When stratified into 5 groups on the maternal index, cows in the very high maternal group had less recorded calving dystocia, superior calf quality, better docility, and superior milk scores (P < 0.05; Table 4). A greater terminal index of the cow was adversely associated with cow docility and milk score when based on an across-breed analysis (Table 2). All producer-recorded traits increased linearly per unit increase in EBV for the respective trait.

Associations with live weight

Both cow live weight and the birth weight of progeny declined with increasing cow maternal index value (Tables 5 and 6); however, once breed was adjusted for in the model, there was no association with birth weight, while cows were expected to get heavier as the maternal index increased (Table 5). The maternal index value was significantly associated with weaning weight when the index was treated as a continuous variable (Table 5).

For every 1 SD unit increase in terminal index, cow weight increased linearly by 23.77 kg (Table 5). Weaning weight increased by 0.61 kg per kg increase in EBV for maternal weaning weight of the cow when breed was not accounted for in the model but this nearly halved once breed was considered in the model. A strong association existed between EBV for cow weight and phenotypic cow weight (Table 5).

Associations with slaughter traits

Although associations existed between the maternal index of the cow and the carcass measurements of her progeny, all regression coefficients were close to zero (Table 5), and little difference was observed between the 5 groups stratified on maternal index (Table 7). Progeny carcass weight, conformation score, and age of slaughter declined linearly by 0.43 kg (P < 0.05), 0.03 units (P < 0.01), and 0.11 d (P < 0.001), respectively, per SD increase in maternal index (Table 5); adjusting for breed in the model reversed some of the associations in that, within breed, selection for increased maternal index was expected to result in heavier and higher conformation carcasses (Table 5). For every SD increase in the terminal index of the cow, carcass traits of progeny improved, with carcass weight increasing linearly by 6.72 kg, conformation score increasing linearly by 0.46 units, fat score reducing linearly by 0.36 units and age at slaughter declining linearly by 3.6 d (Table 5).

For every SD increase in the maternal index of a cow, carcass weight of the cow reduced linearly by 3.03 kg (Table 5). Carcass weight of cows increased linearly by 0.89 kg per kg increase in EBV for cow carcass weight; the expectation was 1. Conformation and fat score of cows increased linearly by 1.02 and 1.62 units per unit increase in EBV for carcass conformation and fat score, respectively.

Discussion

Calf-to-beef production systems, like many agricultural enterprises, are faced with the desire to improve several characteristics concurrently, many of which are antagonistically

Table 4. Mean maternal index (Mat Index) for the 5 groups of maternal index along with the associated mean estimated breeding value (EBV) for direct calving difficulty, maternal calving difficulty, docility, and maternal weaning weight and the associated least square means (SE) for each of the producer recorded traits examined

	Calf quality (1 to 5) 1,5	4.21 (0.023) ^a 4.21 (0.022) ^{ab} 4.23 (0.022) ^{cc} 4.24 (0.022) ^{cd}	4.25 (0.022) ^d
	Milk score (1 to 5) 1.4	3.83 (0.007) ^a 3.88 (0.006) ^b 3.94 (0.005) ^c 4.00 (0.005) ^d	4.07 (0.006) ^e
Phenotypic	Cow docility (1 to 5) 1.4	4.15 (0.007) ^a 4.14 (0.006) ^{ab} 4.15 (0.005) ^{ab} 4.16 (0.005) ^a	$4.18 (0.006)^{c}$
	Docility (1 to 5) ^{1,3}	4.17 (0.007) ^a 4.16 (0.006) ^a 4.18 (0.005) ^a 4.18 (0.005) ^a	$4.18 (0.006)^{a}$
	Dystocia (1/0)²	0.033 (0.005) ^a 0.029 (0.004) ^{ab} 0.028 (0.004) ^b 0.027 (0.004) ^{bc}	0.025 (0.004)°
	Maternal weaning weight (kg)	-5.62 0.94 5.14 9.26	15.84
	Docility (1 to 5) ¹	0.00	0.02
EBV	Maternal calving difficulty (%)	11.74 11.32 11.12	11.00
	Calving difficulty (%)	13.88 11.00 9.84 9.12	8.06
	Mat index (€)	66 136 184 232	306
	Group	Very low Low Average High	Very high

poor quality) to 5 (docile/good milk ability/very good quality). Scale of 1 (aggressive/poor milk ability/very

Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss, where the calf sire's calving difficulty EBV was 8%.

Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss, where the calf sire's docility EBV was 0 and the calf was recorded at 6 mo of age.

Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss and was recorded at 6 mo after calving.

Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss, where calf sire's carcass weight EBV was 20 kg and carcass conformation EBV was 0 and calf was

ecorded at 6 mo of age. •Values within columns with different superscripts differ (P < 0.05)

Table 5. The phenotypic change (SE) in progeny carcass traits, cow carcass traits, and weight traits for each SD unit change in Maternal and Terminal index, and for a 1 unit change in estimated breeding value (EBV) of the respective trait, when adjusted or not for breed; also included is the P-value comparing the regression coefficients with or without breed adjustment

		Maternal			Terminal			EBV	
	No breed adjustment	Breed adjustment	P-value	No breed adjustment	Breed adjustment P-value	P-value	No breed adjustment¹	Breed adjustment¹	P-value
Progeny carcass traits Carcass weight (kg)	-0.43 (0.216)*	0.68 (0.277)*	0.002	6.72 (0.384)**	6.96 (0.570)***	0.726	0.43 (0.018)***	0.45 (0.025)**	0.511
Carcass conformation (1–15) ²	-0.03 (0.008)	0.02 (0.010)	<0.001	0.46 (0.013)***	0.24 (0.020)	<0.001	0.50 (0.012)***	0.77 (0.022)***	<0.001
Carcass fat (1–15) ²	0.02 (0.010)*	0.01 (0.013)	0.270	-0.36 (0.017)***	-0.16 (0.026)***	<0.001	0.59 (0.022)	1.12 (0.034)""	0.530
Age at slaughter	-0.11 (0.008)***	-2.50 (0.588)***	0.880	-3.60 (0.842)***	-13.81 (1.221)***	<0.001	. 1	. 1	
Cow carcass traits Carcass weight (kg)	-3.03 (0.73)""	-0.38 (1.771)	<0.001	21.70 (2.475)***	21.24 (3.527)***	0.122	(080:0) 68:0	1.01 (0.131)***	0.434
Carcass conformation (1 to 15) ²	-0.19 (0.051)""	(0.060)	0.097	1.02 (0.081)""	0.61 (0.116)***	0.003	1.02 (0.068)""	0.89 (0.127)***	0.346
Carcass fat (1 to 15) 2	0.06 (0.072)	0.05 (0.088)	0.959	-0.88 (0.121)	-0.28 (0.172)	0.004	1.61 (0.138)***	1.68 (0.238)***	0.942
Weight traits									
Birth weight (kg)	-0.29 (0.109)"	0.18 (0.131)	900.0	0.34 (0.184)	0.52 (0.289)	0.591	I	I	
Weaning weight (kg)	1.02 (0.407)*	1.70 (0.484)***	0.283	0.52 (0.730)	3.87 (1.026)***	0.008	0.61 (0.036)***	0.38 (0.046)***	<0.001
Cow weight (kg)	-5.75 (1.332)***	4.62 (1.612)***	<0.001	23.77 (2.180)***	33.20 (3.217)***	<0.001	1.00 (0.050)***	1.04 (0.084)***	0.720

Significance of association ***P < 0.001, **P < 0.01, *P < 0.05.

'Missing values where trait EBVs were not available.

Scale of 1 (poor conformation /little fat cover) to 15 (excellent conformation/heavy fat cover).

Table 6. Mean maternal index (Mat Index) for the 5 groups on maternal index along with the associated mean estimated breeding value (EBV) for maternal weaning weight, cull cow and cow live weight, and the associated least square means for each of the weight traits examined

		EBV	1			Phenotypic	
Group	Mat Index (€)	Maternal weaning weight (kg)	Cull cow weight (kg)	Cow live weight (kg)	Birth weight (kg)¹	Weaning weight (kg) ²	Cow weight (kg) ³
Very low	99	-5.62	76	80	44.71 (0.42) ^a	291.1 (1.87) ^a	730 (5.09)ª
Low	136	0.94	64	50	44.27 (0.37)ab	290.9 (1.68) ^a	712 (4.57) ^b
Average	184	5.14	58	40	43.93 (0.28)ab	292.0 (1.39) ^a	702 (3.82) ^b
High	232	9.26	56	34	44.15 (0.25)ab	291.4 (1.32) ^a	706 (3.36) ^b
Very high	306	15.84	52	28	43.55 (0.21) ^b	294.8 (1.23) ^a	702 (2.96) ^b

*Referent cow was parity 3 of median age at calving with no heterosis and no recombination loss, where the progeny sire's calving difficulty EBV was 20 kg, and carcass conformation EBV was 2 and 2 and and 2 and no recombination loss, where progeny's direct weaning weight EBV was 20 kg, and carcass conformation EBV was 2 and 2 and 3 of median age at calving with no heterosis and no recombination loss, where progeny's direct weaning weight EBV was 20 kg, and carcass conformation EBV was 2 and 3 of median age at calving with no heterosis and no recombination loss, where progeny's direct weaning weight EBV was 20 kg, and carcass conformation EBV was 2 and 3 of median age at calving with no heterosis and no recombination loss, where progeny's direct weaning weight EBV was 20 kg, and carcass conformation EBV was 2 and 3 of median age at calving with no heterosis and no recombination loss, where progeny's direct weaning weight EBV was 20 kg, and carcass conformation EBV was 2 and 3 of median age at calving with no heterosis and no recombination loss.

the calf was recorded at 6 mo of age.

Referent animal was parity 3 of median age at calving with no heterosis and no recombination loss and was recorded at 6 mo after calving.
-«Values within columns with different superscripts differ (P < 0.05).

Table 7. Mean estimated breeding value (EBV) for maternal index (Mat Index), carcass weight, carcass conformation, carcass fat score, and cull cow weight for each of the 5 groups (very low, low, average, high, and very high) as well as the least square means for each of the carcass traits observed

			EBV						Phenotypic			
מונטיק	Mat Indev (£)	Carcass	Carcass fat scor	Carcass fat score	Cull cow	Age at	Carcass	Carcass conformation	Carcass fat	Cow carcass	Cow conformation	Cow fat score
droup	(a) vaniii	weigin (ng)	Comotinación (kg)	(CT (C) T)	weigit (AS)	staugitter (u)		(CT OIT)	(CT 01 T)	weigin	(CT O) T)	(CT O1 T)
Very low	99	44	3.12	-0.20	9/	745 (2.36) ^a	389.4 (2.36) ^a	8.29 (0.03) ^a	$8.15 (0.03)^{a}$	$479.1 (4.35)^a$	$10.61 (0.14)^{a}$	$9.83 (0.19)^{a}$
Low	136	38	3.02	-0.04	64	748 (2.07) ^{ab}	387.8 (2.07) ^a	$8.31 (0.02)^{ab}$	$8.14 (0.03)^{a}$	$469.9 (3.95)^{ab}$	$10.35 (0.13)^{a}$	9.75 (0.18) ^a
Average	184	34	3.00	0.02	28	$743 (1.79)^{abc}$	$387.1 (1.79)^{a}$	$8.31 (0.02)^{ab}$	$8.17 (0.02)^a$	$469.7 (3.42)^{abc}$	$10.52 (0.11)^{a}$	$9.72 (0.15)^a$
High	232	36	2.98	0.04	26	741 (1.96)ac	387.9 (1.96) ^a	$8.31 (0.02)^{ab}$	$8.16 (0.02)^{a}$	465.0 (3.87) ^{bcd}	$10.21 (0.13)^{b}$	$10.03 (0.17)^{a}$
Very high	306	36	2.80	90.0	52	740 (2.21)ac	388.1 (2.21) ^a	8.22 (0.03)ac	8.26 (0.03) ^b	457.3 (4.04) ^d	$9.86 (0.13)^{c}$	9.88 (0.18) ^a

Referent animal was a steer from a parity 3 cow of median age at calving with no heterosis and no recombination loss, carcass weight was 360 and a fat score of 7 where sires carcass weight EBV Scale of 1 (poor conformation/little fat cover) to 15 (excellent conformation/heavy fat cover)

Referent animal was a 24-m steer from a parity 3 cow of median age at calving with no heterosis and no recombination loss, sire carcass weight EBV was 40 kg where sire conformation score EBV was 2, sire fat score EBV was 0 for the respective dependent variable was 40 kg and fat score EBV was 0.

Referent animal was a parity 3 cow of median age at calving with no heterosis and no recombination loss

••Values within columns with different superscripts differ (P < 0.05)

correlated. Examples include milk production and fertility in dairy cows (Berry et al., 2016a), growth rate and health in broilers (Buzala and Janicki, 2016), feed efficiency and both carcass leanness and eating quality in swine (Cameron, 1990) and growth rate and baking quality in crops (Laidig et al., 2017). The goal of calf-to-beef production systems is to improve profit via a good quality and efficiently produced carcass from a productive and efficient cow herd. Genetic correlations between most terminal and cow traits tend to be antagonistic (Phocas, 2009; Crowley et al., 2011; Berry and Evans, 2014). Achieving genetic gain for terminal traits can be relatively easy in cattle because, in most instances, the traits are: (1) moderately heritable (Crowley et al., 2011; Englishby et al., 2016) implying that only a small number of progeny records are required to achieve moderate accuracy of selection or generate a sufficiently large reference population for genomic evaluations (Daetwyler et al., 2008), (2) they are not sex-linked and thus can be measured on both males and females, and (3) they do not require a long time horizon for measurement, relative to other cattle traits (e.g., fertility). Therefore, genetic gain in carcass weight and conformation has been relatively rapid in beef cattle (Berry et al., 2016a). Because, however, of the antagonistic genetic correlations between these terminal traits and many female traits, indirect selection has caused a deterioration in female reproductive traits as well as milk yield in beef cattle (Berry et al., 2016a). The most logical strategy to reverse any unfavorable genetic trends in female productive traits is to include all relevant traits in a breeding objective. Of fundamental importance is that genetic gain in maternal characteristics does not, in turn, contribute to a (rapid) deterioration in terminal attributes.

The collapsing of information on genetic merit of individual traits into a single value, often expressed as profit per animal, has long been proposed via selection index theory (Hazel, 1943). Such indexes are particularly advantageous for achieving genetic gain when antagonistic genetic correlations exist among traits limiting the ability to move both traits in desirable directions (Hazel et al., 1994). Selection indexes are now routinely used in dairy cattle breeding (Miglior et al., 2005; Cole et al., 2018), sheep (Santos et al., 2015; Bohan et al., 2019), pigs (Ali et al., 2019; Weishaar et al., 2020), beef (Newman et al., 1992; Connolly et al., 2016), and beef for use on dairy females (Berry et al., 2019). Despite this, few studies have actually attempted to validate these breeding objectives (Coleman et al., 2010; Newton et al., 2017; Berry et al., 2020), especially in beef cattle (Clarke et al., 2009; Connolly et al., 2016), and more specifically for maternal breeding objectives. Based on a validation of the Irish cattle terminal index carried out on 156,864 commercial carcass records, Connolly et al. (2016) reported a 1 unit greater terminal index value was associated with, on average, €1.14 increase in carcass value and 0.035 d decrease in age at harvest. Using a database of 1,131 Irish dairy herds, Ramsbottom et al. (2012) illustrated how each unit increase in the Irish national dairy cow breeding objective was associated with €1.94 extra profit per lactation; the expectation was €2 profit per unit increase in the national index value. The objective of the present study was to quantify if differences in genetic merit for a maternal index in beef cattle at birth translates into differences in subsequent phenotypic performance. Of particular interest also was the ramification of such a selection strategy on the terminal characteristics of the resulting progeny.

Importance of the Irish Maternal Index

In Ireland, national breeding indexes are provided by the ICBF which are an independent body that also manage the national

database (Wickham, 2005). Two national breeding indexes exist in Ireland: the terminal index for the selection of parents to breed animals destined directly for slaughter, and the maternal index for the selection of parents of the next generation of females. A total of 17 traits comprise the Irish maternal index which can be decomposed into what is termed: (1) calf contribution (includes direct calving difficulty, gestation length, calf mortality at birth, carcass weight, carcass conformation, carcass fat, feed intake, and progeny docility), and (2) cow contribution (includes cow survival, calving interval, age at first calving, maternal weaning weight, maternal calving difficulty, cow live weight, heifer live weight, cull cow carcass weight, and cow docility). Within the maternal index, 71% of the emphasis is on the cow contribution, particularly fertility traits, as these are economically important in pasture-based beef herds (Diskin and Kenny, 2014). Since a large proportion of the direct or future descendants are destined for slaughter, 29% of the relative emphasis within the maternal index is attributed to terminal traits (i.e., calf contribution).

A low number of animals with a known sire between the years 2000 and 2008 resulted in erratic genetic trends in this time period. Nevertheless, between 2000 and 2014, the majority of maternal traits trended unfavorably while terminal traits trended favorable as shown by Berry et al. (2016a) and in the present study. This illustrates the necessity of introducing a maternal-based breeding objective in Ireland in 2013. This conclusion is also substantiated in the present study with the estimated adverse associations between many of the femalespecific traits and the Irish terminal index. Selection for the terminal index is expected to delay the age at first calving, lengthen calving intervals, and reduce survival to next lactation; it is also expected to reduce both cow docility and milk score (i.e., less milk). While consideration of such maternal traits within a terminal index is not justified, continued selection for such a terminal index will inevitably erode profitability in the cow herd, which will culminate over generations. While unfavorable associations exist between the terminal index and the female traits leading to a reduction in maternal characteristics, much of the erosion in cow performance from selection on the terminal index is actually due to breed substitution. Continental-type sires (e.g., Limousin and Charolais) tend to rank highly on the terminal index but rank poorly on female performance traits. It is similar for carcass fat, in that a reduction in carcass fat from selection on the terminal index is mainly due to breed substitution, and therefore, leaner breeds are likely to have poorer reproductive performance. This is a likely contributor to the compromised fertility of these animals given the known (phenotypic) association between body condition score (i.e., a subjective measure of subcutaneous body fat) and reproductive performance in beef cattle (Drennan and Berry, 2006). As well as impacting fertility and milk performance, selection on the terminal index is expected to impact the efficiency of the cow herd since each SD unit increase in terminal index value is expected to result in heavier cows.

Importance of validation

There is an onus on scientists to demonstrate that their tools operate in line with expectations, or at least, what the likely deviations from expectation are; animal geneticists are no exception to the rule. Despite this, studies validating either traditional genetic evaluations (Brown et al., 2005; Crews et al., 2006; Twomey et al., 2016) or breeding objectives (Ramsbottom et al., 2012; Connolly et al., 2016; Berry et al., 2020) are lacking in the scientific literature. It is, however, now relatively

commonplace to validate genomic evaluations (Olsen et al., 2011; Saatchi et al., 2012). Nonetheless, validation of overall breeding objectives, in cattle at least, is not well publicized in the scientific literature (Ramsbottom et al., 2012; Newton et al., 2017; O'Sullivan et al., 2019). To our knowledge, only 1 study has evaluated the impact on phenotypic performance from selection on a maternal breeding objective in cattle and this was a relatively small controlled study undertaken in Ireland (McCabe et al., 2019). McCabe et al. (2019) failed to detect a significant difference between a high genetic group (n = 41) and low genetic group (n = 41) for body weight, body condition score, milk yield, and a range of intake traits. Although the present study does demonstrate the impact of the maternal index on individual traits, financial information at a herd-level is lacking to truly validate the index.

Irrespective of whether the maternal index in the present study was represented as a continuous trait or as a class variable with 5 levels, higher maternal index females, on average, calved for the first time at a younger age, had shorter calving intervals and survived longer; the higher index females were also expected to be lighter. Nonetheless, the magnitude of the difference between high and low index animals was relatively small. Large differences in female characteristics among animals differing in an index which also includes terminal traits with 21% relative emphasis, should not, however be expected. The correlation between the calf and cow contribution components of the maternal index in 1,286 high reliability (i.e., >70% reliability) beef AI sires was -0.62; hence, 38% of the variability in the cow contribution is due to differences in the calf contribution.

Nonetheless, the advantage of breeding programs over other approaches to improving cow performance traits (e.g., estrous synchronization and improved diet density) is that breeding is cumulative and permanent. Britt et al. (2018) stated that the top 10 producing US dairy cows in the decade previous to their review produced 10 to 14 SD higher than the mean US yield in 2014; similarly, Lobell (2014) stated that the top yields for maize and soybeans in 2014 were 7 to 9 SD greater than the average in 2014. The difference in mean EBV for calving interval between the very low and very high maternal index groups in the present study was only 5.7 d. This is despite the fact that the withinbreed genetic SD for calving interval in the national genetic evaluation is 4.8 d. The challenge therefore is to develop and foster an efficient and effective national breeding program to generate accurate genetic/genomic evaluations for especially the sex-linked, low heritability traits (e.g., fertility: Berry et al., 2014), and identify the high index males and females taking cognizance of genetic diversity. The ability of the beef sector to achieve genetic gain has already been documented, albeit for terminal traits (Berry et al., 2016a); that ability needs to be harnessed and adapted also to maternal traits. In 2016, the first multibreed genomic evaluation in beef was launched in Ireland. In addition, a monetary incentive was provided for beef producers to genotype females, more extensively phenotype, and to breed and select high maternal index animals. In the present study, accelerated genetic gain in the Irish maternal index was observed since the deployment of these genomic predictions. Genomic predictions for breeding objectives significantly improve the reliability and thus genetic response (Calus et al., 2013), with Berry et al. (2016b) reporting a 16% increase in reliabilities for cow-related traits with the inclusion of genomic information in Ireland's maternal index. Nevertheless, the increase in genetic merit observed in the present study is also likely to be associated with the monetary incentives to select higher maternal index females. Additionally, improvements are relatively small in the present study due to the fact that it was based on the average of the national herd. Improvements would likely be more prevalent in herds with greater selection intensity on the maternal index.

While much focus within the farm gate often revolves around economic efficiency, consideration for animal well-being is of growing interest and importance. Of particular note from the present study was the expected reduction in the incidence of calving events requiring assistance following selection on the maternal index; minimizing dystocia at calving favorably impacts both cow (Mee, 2008) and calf (Barrier et al., 2013) welfare, as well as impacting farm-level economic returns (Berry et al., 2019). The Irish maternal index includes both the direct and maternal components of calving difficulty each with their own economic weight. The Irish maternal index also includes an economic weight for docility which is derived from the cost of increased labor and safety risk with a poorly docile animal (Berry et al., 2019). Although docility may often be overlooked in breeding objectives, ease of management and safety is a desire of all beef producers particularly around calving (Hoppe et al., 2008). Results from the present study signify that higher maternal index animals were recorded by producers to be more docile.

Alternative to the current breeding objective

The notion of generating customized selection indexes is not new (McGilliard and Clay, 1983; Bowman et al., 1996); and of some interest in the present study was that, based on the construction of the current maternal index, both progeny carcass weight and conformation are expected to deteriorate, albeit at a very slow rate. An improvement in the maternal index value of the national herd of even 1 SD (at the current rate of genetic gain of 0.01 SD per year, this will take 100 yr to achieve) is expected to result in a population that has only a 0.44-kg lighter carcass weight and a 0.025-units (scale of 1 to 15) poorer carcass conformation. It should, nonetheless, be remembered that the deterioration in carcass traits in breeding females could be negated by using high terminal index sires; using a sire with a terminal index of 1 SD greater than the mean, would increase carcass weight and conformation score by 4.3 kg and 0.24 units, respectively (Connolly et al., 2016), thus offsetting many years of genetic selection on the maternal index. More importantly, however, is that higher maternal index cows are expected to live longer and thus produce a greater carcass output per lifetime. Because of the greater cow survival of higher index females, the herd is expected to be more mature. Weaning weight (Lubritz et al., 1989; Renquist et al., 2006) and carcass weight (Judge et al., 2019) of progeny from multiparae dams relative to progeny from primiaparae dams are heavier. These combined should negate any small deterioration in carcass weight per progeny from long-term selection on the maternal index.

McHugh et al. (2014) evaluated the phenotypic performance of 38,619 Irish cattle differing in genetic merit for individual fertility, calving, and weaning weight traits; none of the cattle used in that study overlapped with those used in the present study. As was observed in the present study, the phenotypic differences reported by McHugh et al. (2014) deviated from expectations based on genetic merit, but the direction of the association between phenotype and EBV was in line with expectation. Therefore, producers who want to place more emphasis on a particular trait within the framework of the maternal index, because of a deficiency within their herd, can select bulls with confidence to breed the next generation of breeding females that are high in maternal index but also

genetically elite for the particular trait(s) of interest. For example, a herd that is genetically sub-optimal for fertility but excelling in terminal traits can target breeding females superior for calving interval EBV. Nevertheless, placing a greater emphasis on any particular trait will have repercussions for genetic gain in the other traits within the index.

Conclusion

Results from the present study highlight that genetically elite maternal index cows had less calving difficulty, superior fertility performance, lighter carcasses, and live weight, as well as being more easily managed. Progeny of these genetically elite cows were lighter at birth, more easily managed, and maintained acceptable carcass traits. Producers and breeders alike should now have confidence in the ability of a maternal index to improve economic efficiency in the cow herd despite including 17 traits, many of which are antagonistically correlated. The long-term strategy of improving the genetic base of the herd is a worthwhile strategy to achieving year-on-year improvements in efficiencies.

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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