Herd and animal-level management tools generated from national databases and national genetic evaluations

A Thesis Presented for the Degree of
Doctor of Philosophy
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Abbreviations

AFC	Age at First Calving
AI	Artificial Insemination
BFPP	Beef Female’s Profit Potential
BLUE	Best Linear Unbiased Estimates
BLUP	Best Linear Unbiased Predictions
CIV	Calving Interval
CFS	Calving to First Service
CP	Current Parity
CONF	Carcass Conformation
C.O.W	Cow’s Own Worth
Cullcwt	Cull cow carcass weight
CWT	Carcass Weight
DAFM	Department of Agriculture Food and the Marine
DBI	Dairy Beef Index
DMI	Dry Matter Intake
DST	Decision Support Tool
DSS	Decision Support System
E	Environment
EBI	Economic Breeding Index
EBV	Estimated Breeding Value
FP	Future Parity
FR	Friesian
G	Genotype
GBLUP	Genomic Best Linear Unbiased Predictions
G × E	Genotype × Environment interaction
h^2	Narrow sense heritability
H^2	Broad sense heritability
H × E	Heterosis × Environment interaction
HP	Heifer Potential
HO	Holstein
HTD	Herd-Test Day
HYS	Herd-Year-Season
ICBF	Irish Cattle Breeding Federation

IFA	Irish Farmers’ Association
IgG	Immunoglobulin G
IoT	Internet of Things
IT	Information Technology
JE	Jersey
LSM	Least Squares Means
MY	Meuse Rhine Yssel
MOCG	Month of Calving Group
MO	Monthbelliarde
NMP	Nutrient Management Plan
NS	Number of Services
PG	Percentile Group
PTA	Predicted Transmitting Ability
PV	Production Value
Rindex	Irish National Replacement Index
RV	Retention Value
SE	Standard Error
SD	Standard Deviation
SI	Sub-index
SR	Shorthorn
SU	Survival
SMS	Short Message Service
UK	United Kingdom
UCD	User-Centred Design

Statement of Original Authorship

I hereby certify that the submitted work is my own work, was completed while registered as a candidate for the degree stated on the Title Page, and I have not obtained a degree elsewhere on the basis of the research presented in this submitted work

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Abstract for thesis titled "Herd and animal-level management tools generated from national databases and national genetic evaluations"

by Fíona Dunne

Irish cattle-based decision support tools (DSTs) currently focus on breeding and identifying genetically superior parents for future generations and the appropriate bull teams to use; however, one exception being a dairy management DST which ranks dairy cows on their remaining lifetime profitability for voluntary culling. The animal's additive genetic merit forms the basis of all genetic-based DSTs and is estimated by disentangling an observed phenotype into the additive genetic effects from the environmental effects (i.e., BLUEs) and, in doing so, estimates are generated for both. Yet, to date only the additive genetic contribution to an animal performance has been exploited. Moreover, there are clear voids in beef management genetic-based DSTs. The objectives of this thesis were therefore to: 1) characterise best linear unbiased estimated (BLUEs) and quantify the response to selection for additive and non-additive genetic merit by herd BLUEs, 2) construct the framework for a DST for predicting the expected carcass revenue for growing cattle, and 3) develop the framework for a DST to predict the expected remaining lifetime profitability of beef females to identify candidates for culling. Data used within this thesis originated from the national cattle database and the national genetic evaluations. This thesis demonstrated that the response to genetic selection varied depending on the herd BLUE and therefore potential exists for herd BLUEs to be used when tailoring breeding values and DSTs for each individual. Results also substantiate that although the carcass value of an animal is commonly predicted from their recorded breed composition, using the transaction index framework developed, the accuracy of the carcass revenue prediction doubled. This thesis also validated that when beef females were ranked on their expected lifetime profitability, the females identified for voluntary culling contributed €32 less per calving to the herd's profitability relative to the highest ranked females.

Chapter 1: Introduction and Review of the Literature

1.1 Introduction

Decision support systems have revolutionised domesticated animal breeding by means of providing a pathway of scientific knowledge to the end user (Rose et al., 2018) with the objective of supporting the decision-making process. Despite this, voids remain whereby databases are not fully utilised or entire sectors of an industry have been ignored. Dairy cattle genetic evaluations are routinely run in numerous developed countries (Cole and VanRaden, 2018) and, simultaneous to the estimation of breeding values, herd management and environmental effects are disentangled and they themselves estimated. Despite these estimates being readily available, they are largely ignored and discarded. Estimates of herd contemporary group effects have the potential to provide data-driven indications of an individual animal’s response to selection when performing in a given herd environment. Therefore, an opportunity exists to enhance the current decision support tools (DSTs) available by providing complementary information to what currently exists when predicting an animal’s phenotypic performance. The range of DSTs within the Irish beef industry has solely focused on breeding and, despite the existence of a culling DST available in the dairy sector; no such DST has been developed in the beef sector. Furthermore, within the beef industry, there are many different production systems such as finishing systems whereby animals are traded to be finished and therefore the producer does not actually breed these animals. Currently there are no DSTs that support the decision making process when trading growing animals and assist in the identification of superior animals based on their predicted carcass revenue.

The objectives of the present thesis were to investigate novel approaches of utilising existing data originating from the Irish national cattle databases or data which is routinely generated from national cattle genetic evaluations. This tactic was taken to minimise the requirement for collecting data to undertake the research but more importantly to enable rapid and relatively seamless deployment of the knowledge generated within. The application of such data into DSTs was investigated within both the dairy and beef sectors. Within the dairy sector, herd-level best linear unbiased estimates (BLUEs) were characterised and the response to selection for additive and non-additive genetic merit by herd BLUEs quantified. In addition, the framework of two DSTs were developed for the beef sector: firstly, predicting the potential carcass revenue of a beef animal destined for slaughter exploiting both genetic and non-genetic effects;

and secondly, predicting the expected remaining lifetime profitability of candidate breeding beef females to assist in more informed culling decisions.

Chapter 1 summarises the existing literature which documents the developments, as well as the pitfalls, of decision support systems as a whole, the challenges to user-engagement, goal-setting theory and the evolution as well as application of DSTs in animal breeding; the voids in data utilisation and DSTs for both the dairy and beef sector are also reported. The associations between a number of herd-level characteristics and herd BLUEs are quantified and reported in Chapter 2. Chapter 3 quantifies the response to selection on additive and non-additive genetic merit conditional on the herd's BLUE metrics for a given trait. Results suggest that the response to selection on additive and non-additive genetic merit for a given trait do in fact differ by herd BLUE. Therefore, an opportunity exists for herd BLUEs to be utilised in the decision support process of selecting parents of the next generation but also potentially on putting a value on individual animals using the frameworks developed in Chapter 4 and 5. A framework was developed in Chapter 4 to predict the carcass revenue potential of beef animals that will never become parents by exploiting both genetic and non-genetic effects; such results can be used to provide transparency when purchasing animals, especially at a young age when phenotypic differences are yet to be realised. In Chapter 5, an index was developed to enable the ranking of candidate breeding beef females based on their remaining lifetime production; the results from the study can be used to facilitate the decision making process of which cows to cull by providing data-driven decision support. Together with Chapter 4, the breeding beef ranking index can be used to decide, at a young age, whether a heifer should enter a feeding regime for slaughter or a feeding and breeding regime to become a replacement heifer. The thesis is summarised in Chapter 6, alongside the implications and conclusions of the presented body of work.

1.2 Decision Support Systems

The development and incorporation of decision support systems (DSS), especially in the agricultural sector, has intensified globally in the past 20 years. A survey carried out by Rose et al. (2016) suggested that, at that time of carrying out the survey, there were approximately 395 DSTs available to UK farmers, clearly demonstrating the vast choice of DSTs available. The general definition of DSS tends to be software-based technology that facilitates and provides support in the decision-making process (Matthews et al., 2008; Jakku and Thorburn, 2010; Rose et al., 2016; Oxford University Press, 2019); both Cox (1996) and Rose et al. (2016), however, suggested that the definition of DSTs should be broadened and can, in fact, be presented in many forms including: 1) human-based (i.e., farm advisors), 2) paper-based (i.e., maps), 3) SMS and email alerts and 4) mobile-phone apps. Matthews et al. (2008) described the distinction between a DST and a DSS as a DSS is "not only a standalone software tool but also data, encapsulated knowledge and facilitates to communication or interpret"; throughout the literature, however, both DSS and DST tend to be used alternatingly. The fundamental purpose of agriculturally-focused DSTs is to provide a pathway of scientific knowledge to the end-user (i.e., the farmer or farm advisor), thereby providing a solution to a problem (Lindblom et al., 2017; Rose et al., 2018). In doing so, DSSs interpret data and apply the appropriate analyses and, in turn, assist in the identification of evidence-based solutions that aid the decision making process (Dicks et al., 2014; Rossi et al., 2014; Rodela et al., 2017). A crucial component to the success of DSTs is that they are easy to understand and although perhaps sometimes be taken for granted, most importantly they must provide a solution to an actual problem.

The Irish agricultural industry was actually the forerunner industry in the adoption of computer technology when the first computer in Ireland was purchased by The Irish Sugar Company in 1958 (Óriain, 1997) to calculate payment statements for beet growers. A range of specialist DSTs currently exist for both Irish farmers and farm advisors, providing support in the decision-making process regarding questions around land, nutrition and animal breeding. The Nutrient Management Planning (NMP) online tool, for example, is a DST available to farm advisors to assist in quantifying the nutrient status of land and, by extension, fertiliser management strategies are also generated to assist in nutrient management. PastureBase Ireland is an online DST available to Irish farmers facilitating the recording of various performance indicators such as grass cover and fertiliser applications; the dual-purpose DST then generates reports such as grazing rotation planners (i.e., the grass wedge) that aids in the decision-making process whilst simultaneously capturing data that can be used for research purposes (Hanrahan et al., 2017). DSTs in the form of breeding objectives are routinely used by Irish dairy, beef and sheep farmers when making breeding decisions. These DSTs are constantly evolving in line with industry demands. For instance, an extension of the national dairy breeding index, the ‘Cow’s Own Worth’ (Kelleher et al., 2015) index, was developed to rank dairy females based on their remaining lifetime profit thereby assisting in culling decisions.

1.2.1 Decision support tool engagement

Despite the obvious abundant availability of DSTs to producers, user engagement continues to be an obstacle to their uptake. Rose et al. (2016) reported that of 244 individuals surveyed in the UK, 49% were using DSTs, 28% of which were software-based, 22% were paper-based, and 10% were apps. On one hand the behaviour of the end-user towards the DST is an obstacle to overcome; on the other hand, the objective, application and delivery of the DST can in itself, lead to the demise of the DST. Within the field of social science, there is a generalisation that an individual’s behaviour tends to be dictated by their goals (Custers and Aarts, 2005). Furthermore these goals may not necessarily be consciously pursued (Bargh et al., 2001); therefore if an individual does not see the usefulness of a particular DST as a method of achieving their goal, then there is no obvious reason to engage with the DST.

Within the theory of planned behaviour, Ajzen (1991) suggests that a person’s intention contributes to performance and a person’s intention is influenced by three independent factors: 1) *attitude towards behaviour* i.e., a person may evaluate how favourable or unfavourable the adoption of a new DST is to their business; 2) *subjective norm* i.e., the social and peer pressure a person may experience to adopt or perhaps, not adopt a new DST; and, 3) *perceived behavioural control* i.e., the ease or difficulty experienced when using a DST. Rose et al. (2016) agreed with the suggestions made by Ajzen (1991), also stating that core factors that influence the use of DSTs include performance expectancy, peer recommendation, and ease of use. Trust in the DST, the cost of the DST and the age of user are also known factors influencing the uptake of DSTs (Rose et al., 2016).

Interestingly, the age of the user was a big factor in the integration of software-based DSTs on-farm and was closely linked to IT education as some of the older generation were reported to not own a computer or be “half afraid of computers” (Rose et al., 2016). Research by Morris and Venkatesh (2000) into the link between age and technology adoption using Ajzen (1985) theory of planned behaviour reported that, in the short term, subjective norm is more important in the adoption of new technology for older workers;

in contrast, the younger workers' attitude towards the new technology was more important than subjective norm. It was hypothesised that younger workers may have had more exposure to technology and therefore are more likely to make independent decisions towards its adoption. Older workers on the other hand, are more comfortable in the application of traditional methods for job completion and therefore seek the opinions of co-workers before adopting new technology (Morris and Venkatesh, 2000).

In Ireland, currently less than 45% of the farming demographic are under the age of 55, with the average age of Irish farmers being 57.5 years (DAFM, 2018b), therefore subjective norm may be a huge contributing factor in DST user-engagement in Ireland. Results from an investigation carried out by the Irish Farmers Association on the usage of farm technology in Ireland whereby 710 agri-stakeholders were questioned, suggest that agricultural media had a larger influence on the adoption of technologies relative to farm advisors, peers, and even discussion groups (IFA Farm Business Skillnet Research Study, 2019). Nevertheless, discussion group participation in the farming community is still a potential method of establishing positive peer behaviour towards the adoption of new DSTs as well as providing an opportunity to train individuals on a new DST. The importance of facilitating training was highlighted in the IFA Farm Business Skillnet Research Study (2019) which reported that over 50% of the participants stated that they not only did not feel confident in using technology, but over 60% said that access to training was in the top three barriers to the adoption of technology. Figure 1.1 illustrates a force field analysis adapted from the key factors that Rose et al. (2016) suggests influence the use of DSTs.

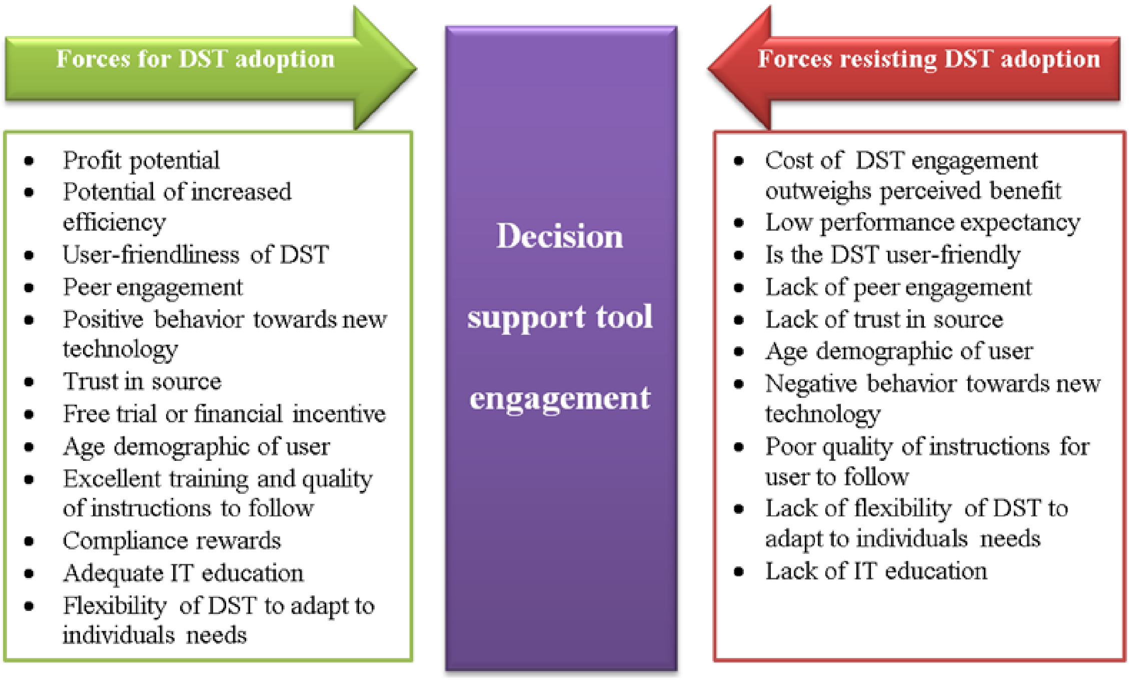

Figure 1.1: Force field analysis of decision support tool user engagement.

The behaviour of the end-user is, however, only partially responsible for the poor uptake in DSTs; Rossi et al. (2014) attributes the remaining proportion of responsibility to the technical limitations of the DSS. The lack of DST engagement is unfortunately not a new phenomenon and was reported by McCown (2002) almost two decades ago. One such limitation of the DSSs available is that they are often focused on providing solutions for one particular problem (e.g. breeding for genetically superior animals for fertility), whereas the problem may only be one element in a multicomponent production system (e.g. poor heat-detection or nutrient deficiencies post-partum). Therefore, the end-user must have a holistic view of all production systems as issues tend to be interconnected (Rossi et al., 2014). Bridging the gap between the researchers that develop DSTs and the end-users is becoming increasingly important and crucial to the on-going engagement with the DST. Lindblom et al. (2017) reported that the level of stakeholder involvement in the DSS development has a major bearing on the success or failure of the DSS. One method of addressing the lack of user involvement would be to adopt user-centred design (UCD), an approach which involves the end-user throughout the development process in order to gain access to the decision-making environment (Lindblom et al., 2017; Rose et al., 2018).

1.2.2 Goal-Setting Theory

As the data pool available for analyses continues to grow in today's age of "big data", with it expands the potential scope of research as well as the obstacles of complete data utilisation. With such a vast amount of data available from DSTs, the end-user may find it increasingly difficult to identify and set achievable goals. Moreover, depending on the type of goal set, the results may be bidirectional in performance outcomes (i.e., the set goal may have positive or negative implications on performance). For instance, learning goals require the individual to acquire knowledge in order to complete the goal which, in turn, facilitates metacognition (Locke and Latham, 2006). When the outcome of a goal is too specific, the individual may be too focused on reaching the set-goal and disregard the learning opportunity attainable in the process of reaching the goal (Locke and Latham, 2006). An example of where the outcome of the goal was prioritised over the method of achieving the goal would be if the goal was to artificially inseminate 90% of the dairy herd within the first 3 weeks of the breeding season; one may become fixated on the number of cows inseminated rather than inseminating the cows effectively to ensure the highest pregnancy rate is achieved. Conversely, as the specificity of goals reduces, the variability in performance widens (Linderman et al., 2003). Therefore a decision by the goal setter must be made as to what the individual should achieve when reaching the goal, be it a learning opportunity or task completion. Furthermore, how people interpret goals can be detrimental to their achievement due to the 'framing effect' in psychology whereby, depending on how a goal is presented, some goals can be viewed as threatening or motivating. Locke and Latham (2006) reviewed approximately 400 studies during the development of goal-setting theory and concluded that, in order to achieve a higher level of performance, goals set out must be specific and difficult rather than easy and vague. At the same time, if a goal is thought to be too difficult and unattainable due to the goal's framing effect, individuals may tend to apply little effort and therefore their performance is compromised (Locke and Latham, 2006).

As suggested by Shim et al. (2002), the three traditional fundamental characteristics of DSS are: 1) a well-developed database that has access to various forms of information, 2) mathematical modelling functions, and 3) a simple user-friendly interface. These characteristics are intrinsic to the success of the Irish dairy Economic Breeding Index (EBI) DST and its growth in usership over the past two decades, which in turn has led to the accumulation of information resulting in an internationally unrivalled database.

Through the provision of evidence-based information, presented in a simple manner, users of the EBI have been able to utilise the information available, set achievable goals, and make more informed decisions when breeding their animals in order to increase the profit achievable from future progeny. Production and fertility are the two largest sub-indexes within the EBI, both of which each represent 34% of the overall emphasis. The average EBI figure for Irish dairy cattle in the past decade from just over €17 in 2010 to just under €96 in 2018 (ICBF, 2019d). The success of the EBI as a DST is reflected in the year on year improvement in the genetic merit of Irish dairy animals since its introduction (Figure 1.2). Furthermore, the fertility sub-index has continued to improve which has materialised in an ever-improving phenotypic calving interval (Figure 1.2).

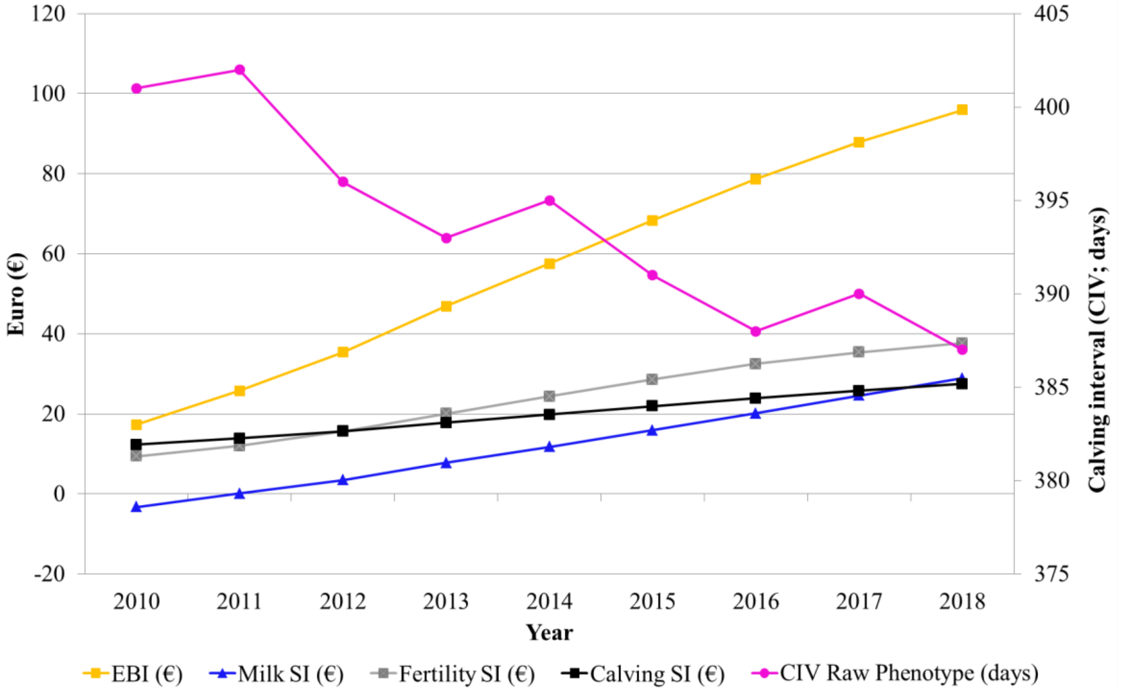

Figure 1.2: Genetic trends between the years 2010 to 2018 (inclusive) for the Economic Breeding Index (orange), milk sub-index (blue), fertility sub-index (grey), calving sub-index (black) (figures derived from ICBF (2019d)) and, the average phenotypic calving interval (CIV; pink) (figures derived from ICBF (2019c)).

1.3 Animal Breeding Decision Support Tools

Since the domestication of animals, breeders have practiced selective breeding, although the initial emphasis may have been on the aesthetics of the animal rather than actual producing ability (Cole and VanRaden, 2018). In the late 1940s to early 1950s, C.R. Henderson revolutionised animal breeding programs with the development of various statistical models (Henderson, 1949; Henderson, 1953; Henderson et al., 1959). Henderson recognised that one could not identify the causes of changes in phenotypic performance by merely comparing changes in herd averages from one year to the next. He suggested that the environmental and genetic factors that contribute to phenotypic performance must be separated in order to effectively assess a breeding program. In doing so, by partitioning the causative factors one was able to establish whether changes were due to improvements in environmental factors (e.g., nutrition and management) or the genetic factors of the herd, or perhaps a combination of both. Visscher et al. (2008) stated that the observable phenotype (*P*) is the sum of both the unobservable genotype (*G*) and unobservable environment (*E*), their interaction (*G*E*) and their joint variability (*G*,*E*) where:

$$P = G + E + G * E + G, E$$

Furthermore, the variance of the observed phenotypic performance (σ_p^2) is the sum of the unobservable genetic (σ_g^2) and environmental (σ_e^2) variances as well as both the genotype by environment covariance ($\sigma_{g,e}$) and the interaction between the genotype and environment (σ_{g*e}^2) (Visscher et al., 2008):

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2 + 2\sigma_{g,e} + \sigma_{g*e}^2$$

Despite this widely accepted partitioning of phenotypic variance into its respective contributing factors, both the genotype by environment (G × E) interaction and the associated covariance are often ignored and omitted from phenotypic modelling due to the difficulty in estimating them (Visscher et al., 2008). In general, genetic evaluations tend to strive towards the identification of animals that will achieve superior performance in the average environment (Haile-Mariam et al., 2008); consequently, recommendations from genetic evaluations are applicable to the average population. Nonetheless, G × E interactions can result in reranking or scaling effects, the former causing more issues in breeding programs. Reranking occurs when animals rank differently in different environments whereas scaling effects occur when animals perform at different levels in different environments, but their ranking remains consistent (van der Laak et al., 2016) (Figure 1.3).

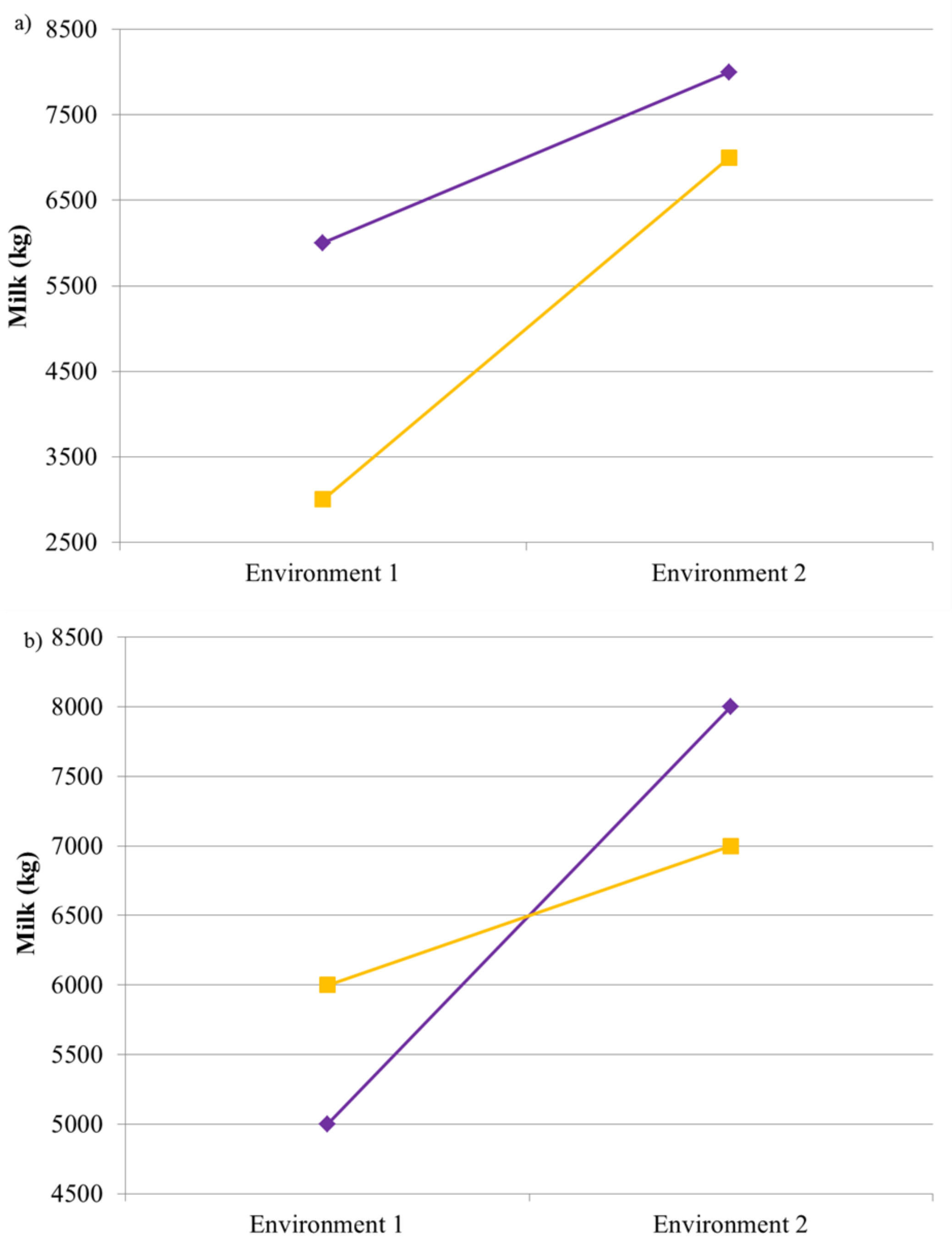

Figure 1.3: Genotype by Environment interactions resulting in (a) scaling effects and (b) re-ranking effects due to the performance of animal 1 (purple line) and animal 2 (orange line) in two different environments.

A slight scaling effect, though not significant, was reported in Coleman et al. (2010), whereby the performance of three strains of Holstein-Friesians were investigated on two different feed system environments which differed by stocking rate and concentrate input. The high genetic merit animals (i.e., high EBI figure) tended to perform better than the low EBI animals, regardless of the environment. Yet when comparing the same genetic merit cohort across the two different environments their performance was not consistent (Coleman et al., 2010). Therefore even though the level of performance of animals with the same genetic merit can vary in different environments, animals with superior genetic merit tend to outperform animals of inferior genetic merit when comparing them in the same environment.

A similar study which investigated the presence of a G × E interaction was carried out by McCarthy et al. (2007) whereby the performance of three different genetic strains of Holstein-Friesian animals were compared in three different feed systems environments. Irrespective of the environment, there tended to be a significant difference between the performances of the three different strains of Holstein-Friesians (Table 1.1) which were characterised as either: 1) high milk producers (HP; high production), 2) robust for many traits (HD; high durability) or, 3) of New Zealand genetic merit (NZ; New Zealand). Both re-ranking and rescaling events were reported in McCarthy et al. (2007), although not always significant. For instance, the HP stain was reported to have significantly superior nadir body weight in the high grass allowance diet than the HD strain, yet no differences existed in the remaining two environments (Figure 1.4; a). Moreover, a significant G × E interaction was reported to exist for body weight gain in the breeding season which resulted in scaling effects whereby animals within the same genetic stain cohort performed significantly different in each environment (McCarthy et al. 2007; Figure 1.4; b).

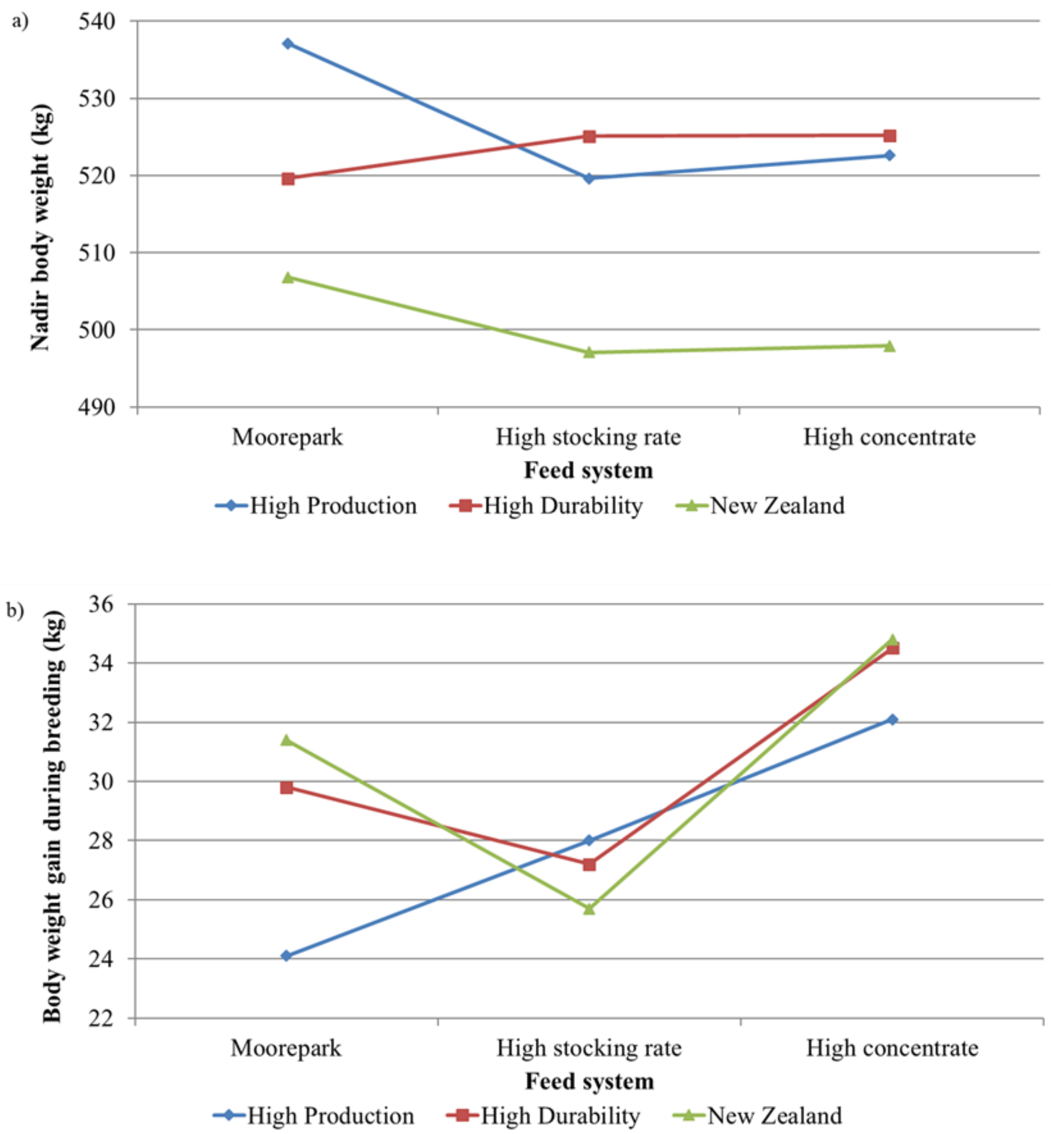

Figure 1.4: Re-ranking and re-scaling effects of three genetic strains of Holstein-Friesian, namely high production, high durability and New Zealand, performing in three different feed system environments (i.e., high grass allowance (Moorepark), high stocking rates, and high concentrate allowance) on nadir body weight (kg; a) and body weight gain during breeding (kg; b) (McCarthy et al., 2007).

Table 1.1: Effect of genetic stain of Holstein-Friesian and feed system (MP, HS, and HC)[1] on body weight parameters (McCarthy et al., 2007).

	Holstein-Friesian strain and feed system												
	High Production			High Durability			New Zealand				Significance[2]		
Variable	MP	HS	HC	MP	HS	HC	MP	HS	HC	SE	S	F	S × F
Calving (kg)	615.7	616.8	607.6	597.6	597.8	606.6	583.4	573.4	579.2	7.43	0.001	0.77	0.56
Dry off (kg)	606.4	607.8	633.1	621.6	614.2	641.6	592.7	581.5	608.2	6.95	0.001	0.001	0.79
Average (kg)	563.0	552.6	569.4	566.8	565.6	573.5	529.6	534.3	539.1	5.58	0.001	0.01	0.35
Nadir (kg)	537.1	519.6	522.6	519.6	525.1	525.2	506.8	497.1	497.9	5.67	0.001	0.78	0.05
DIM to nadir (kg)	58.6	55.7	52.1	53.0	53.1	51.3	51.8	56.8	52.3	1.78	0.16	0.05	0.13
Loss to nadir (kg)	83.3	91.3	81.5	79.0	72.2	78..1	84.0	78.0	80.0	3.91	0.05	0.64	0.18
Gain postnadir (kg)	77.3	89.6	99.8	92.9	85.3	108.1	96.8	81.9	108.3	4.37	0.10	0.001	0.05
Gain during breeding (kg)	24.1	28.0	32.1	29.8	27.2	34.5	31.4	25.7	34.8	1.58	0.07	0.001	0.02

[1] MP = Moorepark feed system; HS = high stocking rate feed system; HC = high concentrate feed system.

[2] S = effect of strain of Holstein-Friesian; F = effect of feed system; S × F = effects of interaction between strain of Holstain-Friesian and feed system.

Mulder et al. (2006) suggested that if genetic correlations between environments are < 0.61 then specific breeding programs may be worth consideration. For this reason, whilst investigating dairy cattle, Haile-Mariam et al. (2008), van der Laak et al. (2016) and Craig et al. (2018) suggested that little G × E interactions were occurring as the genetic correlations between environments tended to be stronger than 0.81 for traits associated with fertility (Haile-Mariam et al., 2008; Craig et al., 2018) and production (Haile-Mariam et al., 2008; van der Laak et al., 2016). However, herd environments ranked based on fertility performance by Craig et al. (2018) were reported to have greater genetic variance in the lower-fertility dairy herds as well as a greater response to selection relative to high-fertility herds; this suggests that when selecting for improvements in genetic merit for fertility traits, larger gains are possible in low-fertility dairy herd environments (Craig et al., 2018).

1.3.1 Best Linear Unbiased Predictions (BLUPs) and Estimates (BLUEs)

Henderson et al. (1959) proposed a method of analysing animal records that would simultaneously disentangle environmental effects from genetic effects and, in doing so, generate estimates for both. This method involved the use of linear mixed models to estimate the maximum likelihood of fixed effects within the linear mixed model (Henderson et al., 1959). Fixed effects are variables in which the individual levels are specific and constant, such as sex which is either male or female (Kirkwood and Sterne, 2003). Random effects represent a sample of the levels from a population and therefore represent the variation within that population (Kirkwood and Sterne, 2003). Linear regression models are used to estimate the relationship between an explanatory variable and a dependent variable using the best-fitted straight line (i.e., the regression line); this relationship does not necessarily imply a ‘cause and effect’ relationship but can reveal an ‘associated’ effect.

The linear mixed model equation Henderson proposed was:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Zu} + \boldsymbol{e}$$

where $\boldsymbol{y}$ = the observable vector of phenotypic performance, $\boldsymbol{\beta}$ = the vector of fixed effect parameters, $\boldsymbol{u}$ = the vector of random animal effects, $\boldsymbol{e}$ = the vector of random residual effects, $\boldsymbol{X}$ and $\boldsymbol{Z}$ = incidence matrices which relate to records of fixed and random animal effects, respectively (Mrode, 2014). Years later this method of estimating environmental factors (Best Linear Unbiased Estimations; BLUE) and predicting breeding values (Best Linear Unbiased Predictions; BLUP) would be internationally referred to as the BLUP method and has become the most widely used method of genetic evaluation (Mrode, 2014). BLUP-type approaches are still used today in many species that exploit genomic information in their genetic evaluations (Meuwissen et al., 2001; VanRaden, 2008). The BLUP method utilises information from various sources in order to estimate breeding values; animals, therefore, do not necessarily require their own phenotypic information to acquire an EBV. As detailed in Simm (1998), data sources include: 1) the animal's ancestors (i.e., pedigree information), 2) the individual animal, 3) the animal's siblings (both full and half siblings) and, 4) the animal's own progeny. The characteristics of BLUP and BLUE are, as stated by Robinson (1991), as follows:

Best – Calculates the best estimate i.e. resulting in the strongest correlation between the true and estimated breeding value and the smallest mean square error,

Linear – The estimate is a linear function of the observation,

Unbiased – The average of the estimate is equal to the average of the quantity being estimated,

Prediction – Predicts the random effects,

or,

Estimates – Estimates of the fixed effects.

Through disentangling the genetic component from the environmental component as well as other systematic effects (e.g. the animal's sex) responsible for the phenotypic performance, the BLUP method generates estimates of the additive genetic component of each animal (i.e., the animal's estimated breeding value; EBV). Thus, selection on EBVs is more sensible than raw phenotype as it estimates the animal's genetic merit for a given trait in the average environment as nuisance variables within the model are adjusted for. Within genetic evaluations, contemporary group effects such as herd-year-season (HYS) tend to be the main environmental effect captured (Visscher and Goddard, 1993). Traditionally, it has been BLUPs that have always been used in DSTs and BLUE solutions have largely been discarded**.** Despite this, a small number of studies in dairy (Bastin et al., 2009) and beef (Englishby et al., 2017) cattle proposed that contemporary group effects could form an integral part of a DST. Bastin et al. (2009) suggested that dairy cow nutritional advice could be provided at the herd level using retrospective data consisting of herd × test-day (HTD) contemporary group effects from milk urea models. The integration of such information into a milk recording report could facilitate more informed decisions regarding nutrition by herd managers. Within the beef industry, Englishby et al. (2017) reported that finishing herd-year contemporary group effects accounted for between 31% to 71% of the total phenotypic variance for carcass weight. As contemporary group BLUEs are calculated independently of the animal's genetic merit, the use of BLUEs as a descriptor of the herd environment in genotype-by-environment studies could also prove to be extremely informative.

1.3.2 Selection Indexes

Prior to the development of Henderson's BLUP method, both Hazel and Lush developed selection index methodology and what was proposed in 1942 still remains the fundamental basis of selection index DSTs in animal breeding today. Hazel and Lush (1942) proposed three factors that must be known and included in a selection index in order to achieve maximum genetic improvement; 1) the relative (economic) value of each individual trait, 2) the heritability of each individual trait and, 3) both the environmental and genetic correlations among the traits. DSTs in animal breeding have married both Henderson's and Hazel's proposals by adapting the method of predicting additive genetic effects of individual animals and multiplying the (estimated) breeding values for an individual trait by the respective (economic) weight. Selection indexes are calculated as follows:

$$I = b_1X_1 + b_2X_2 + b_3X_3 + \cdots + b_nX_n$$

where I = the selection index; b_i = the partial regression coefficient for trait i; X_i = the phenotypic observation of trait i used in the calculation of EBVs. The selection index is used to maximise the response in the selection objective which is calculated as:

$$H = a_1Y_1 + a_2Y_2 + a_3Y_3 + \cdots + a_mY_m$$

where H = the selection objective; a_i = the economic value for trait i; Y_i = the traits that have been chosen to improve. Economic values have been defined by Hazel (1943) as “the amount by which profit may be expected to increase for each unit of improvement in that trait”. Economic weights can be subsequently calculated as the product of the economic value and the discounted genetic expression (Amer et al., 2001). In the past, single trait selection was commonly practiced, especially in the dairy industry, and although the level of milk produced per cow increased, reproductive efficiency was eroded (Lucy, 2001). This erosion in reproductive performance was concluded to be partially due to the antagonistic genetic correlation between milk production and reproduction (Lucy, 2001), which appears to be a common problem in single-trait selection (Cole and VanRaden, 2018). Multiple-trait selection indexes became the industry standard in animal breeding and, in turn, led to the establishment of a more holistic approach to animal breeding thus counteracting the antagonistic relationships among traits. Cole and VanRaden (2018) documented the individual trait components that are included in the breeding objectives of 21 dairy indexes across the world in Figure 1.5.

When developing multiple-trait indexes, it is important to consider the usability of such a DST and how the end-user will interact with the index. Selection indexes are used to simplify the identification of superior animals by comparing individuals based on their EBVs for individual traits all summed up into a single value per animal (Amer et al., 2001). Splitting selection indexes into smaller sub-indexes also ensures ease-of-use (Cole and VanRaden, 2018). Provided the function of each sub-index is understood, users can make more targeted progress in accordance with their own breeding goal without necessarily understanding each individual trait within the sub-index. In spite of this, the user also has the option to scrutinise an animal’s genetic merit for any given trait underpinning the index if so desired. The Irish dairy economic breeding index comprises 7 sub-indexes and 19 breeding objective traits.

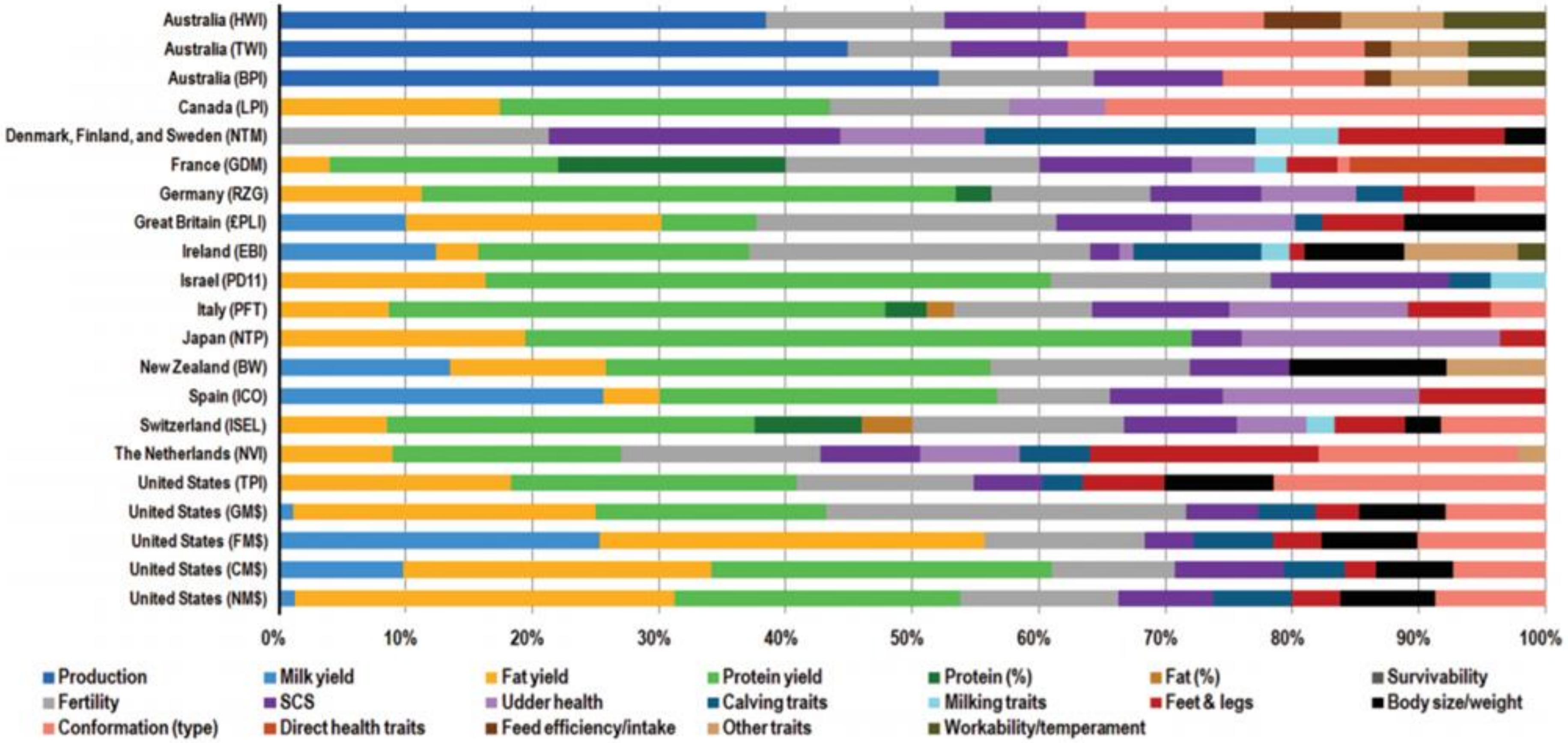

Figure 1.5: Traits included in the breeding objectives of 21 total merit indices of the United States and 16 other countries as reported by Cole and VanRaden (2018).

1.3.2.1 Heritability

Since the formal introduction of the term ‘heritability’ into the scientific community by J. L. Lush in 1940 (Visscher et al., 2008), it has become a fundamental statistic within the field of quantitative genetics and was quickly referred to as one of the main factors to be included in a selection index (Hazel and Lush, 1942). Heritability can be sub-divided into either the broad-sense (H^2) or narrow-sense heritability (h^2), where the proportion of total variance for a particular trait is attributable to either the total genetic variation or the additive genetic variation, respectively (Visscher et al., 2008). Narrow-sense heritability tends to be the statistic commonly referred to in the animal breeding literature unless otherwise stated (Berry et al., 2019b). This is because additive genetic variance is a fundamental element in the application of breeding programs given that, when estimating breeding values, only the contribution of additive allele effects are considered since alleles, and not allelic combinations, are transmitted to the offspring (Aliloo et al., 2017; Rutkoski, 2019). In other words, heritability is a reflection of the relationship shared between the phenotype and the breeding value. Byers (2008) also defined additive genetic variance as “the deviation from the mean phenotype due to inheritance of a particular allele and this allele’s relative (to the mean phenotype of the population) effect on the phenotype”. Narrow-sense heritability has been reported to be the fraction of phenotypic variation within a population which is determined by the genes transmitted directly or inherited from the parents, without taking the mate of the animal into account (Falconer and Mackay, 1996; Berry et al., 2019b). Narrow-sense heritability is estimated as follows:

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

where h^2 = the narrow-sense heritability estimate; σ_A^2 = the additive genetic variance and σ_P^2 = the total phenotypic variance within a population. Whilst the broad-sense heritability statistic is not commonly discussed in the animal breeding literature, the total genetic variance component within the statistic consists of dominance and epistatic variance in addition to additive genetic variance in the numerator. The non-additive genetic variance referred to as dominance variance is the interaction between alleles at the same locus, whereas epistatic variance is the interaction between alleles at different loci (Su et al., 2012). Arguably the most exploited form of non-additive genetic variance in animal breeding protocols has been heterosis, i.e., the effects of crossbreeding whereby individuals of different breeds are mated resulting in a progeny with an expected increase in heterozygosity (Swan and Kinghorn, 1992). Results of crossbreeding tend to be favourable, as the progeny's performance surpasses the mid-parent mean. Heterotic effects, however, are not transmitted directly from parents to the progeny and therefore are not included in the estimation of EBVs.

Importantly, heritability is population specific and therefore, although heritability estimates for a particular trait may be similar, a heritability estimate in one population should not be used as the heritability of the same trait in a different population (Visscher et al., 2008). Due to the fact that heritability is a ratio, both the numerator and denominator are important. When the heritability of a trait is reported to be high, relative to a lowly heritable trait, it does not necessarily mean that the additive genetic variance is larger (Visscher et al., 2008). For instance the total phenotypic variance (denominator) could possibly be smaller and therefore, of the observed variation, a larger proportion of the variation is caused by genotypes. When predicting breeding values, highly heritable traits (e.g. growth traits) require fewer recorded phenotypes for accurate predictions; lowly heritable traits can overcome this obstacle by having a larger number of recorded phenotypes from many progeny in order to accurately predict breeding values. Thus, irrespective of whether a trait highly or lowly heritable, genetic improvement is possible.

1.3.3 Evolution of Genetic Evaluation Modelling

The basic linear mixed model proposed by Henderson et al. (1959) has evolved since its introduction to account for an increasing amount of data as it becomes available; with each adaptation, however, the fundamental framework proposed by Henderson et al. (1959) remains intact. Models are now capable of incorporating more complicated effects to account for factors such as different breeds, maternal effects and correlated traits (Van der Werf, 2002).

1.3.3.1 Sire model

Sire models were commonly used in the early adoption of the BLUP method (Mrode, 2014). This was primarily due to limitations of computational power at the time and the fact that sire models have fewer equations to solve in comparison to the animal model as only the sire effects are fitted to progeny records (Van der Werf, 2002; Mrode, 2014). However, the EBVs derived from a sire model tend to be less accurate and potentially biased. Potential bias can arise as the model assumes that genetic differences between the dams (i.e., the sires mate) do not exist, despite the fact that over time, a sire's mate may not only be a different breed but also have a superior genetic merit (Van der Werf, 2002). Furthermore, EBVs for females cannot be generated from sire models.

1.3.3.2 Reduced animal model

Within a reduced animal model, equations are only set up for parents that have progeny records; therefore the process of estimation requires less computational power than the standard animal model as fewer equations have to be solved (Van der Werf, 2002). Subsequently, by back-solving from the predicted parental breeding values, the estimated breeding values for the remaining animals within the dataset can be calculated (Mrode, 2014).

1.3.3.3 Single trait animal model

For an animal model, a breeding value is fitted for each animal within the dataset; therefore there are an equal number of equations to solve as the number of animals within the dataset (Mrode, 2014). The single trait animal model only consists of one trait of interest, hence named 'single trait', fixed effects (e.g. contemporary group effects) and a single random effect (i.e., the breeding value) are also included (Van der Werf, 2002). The mixed model equation for a single trait model is:

$$\begin{bmatrix} \boldsymbol{X'X} & \boldsymbol{X'Z} \\ \boldsymbol{Z'X} & \boldsymbol{Z'Z} + \boldsymbol{A^{-1}}\alpha \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{b}} \\ \hat{\boldsymbol{a}} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X'y} \\ \boldsymbol{Z'y} \end{bmatrix}$$

where $\boldsymbol{X}$ is the matrix relating to the fixed effects (e.g. sex, contemporary group and twin effects); $\boldsymbol{Z}$ is the matrix that relates records to the animals; $\boldsymbol{y}$ is the vector of observations; $\boldsymbol{A^{-1}}$ is the inverse of the numerator relationship matrix (i.e., thus accounting for the additive genetic relationship between animals); α is the ratio or error variance (i.e., the ratio of residual variance to additive genetic variance); $\hat{\boldsymbol{b}}$ is the solution for the fixed effects; and $\hat{\boldsymbol{a}}$ is the random effect solution (Mrode, 2014).

1.3.3.4 Repeated records model

Mixed models evolved to the repeated animal model in order to account for incidents whereby an individual has more than one record available (i.e., repeated records) for a single trait, such as milk yield records or litter sizes for multiple lactations or pregnancies. Within the model, both temporary (common environmental effects) and permanent (between the records for the individual) environmental effects are accounted for (Mrode, 2014). Therefore, if a dairy cow was to lose the function of a teat due to an accident, it would not impact her predicted transmitting ability value as this would not impact her progeny's performance; losing the function of a teat would, however, impact her permanent environment. The model typically applies some assumptions to the calculations such as the genetic correlation between an individual's records is assumed to be 1 (Mrode, 2014). The linear model equation for a repeated records model is:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{Wpe} + \boldsymbol{e}$$

where $\boldsymbol{y}$ is the vector of the observation; $\boldsymbol{b}$ is the vector of fixed effects; $\boldsymbol{a}$ is the vector of additive genetic random effects; $\boldsymbol{pe}$ is the vector of permanent environmental effects; $\boldsymbol{e}$ is the vector of residual effects; $\boldsymbol{X}$, $\boldsymbol{Z}$ and $\boldsymbol{W}$ are the incidence matrices relating to records of fixed, random, and permanent environmental effects, respectively (Mrode, 2014).

1.3.3.5 Maternal effects model

Maternal effects models encompass both the prenatal and postnatal influences that a mother will have on her young (Falconer and Mackay, 1996). This influence extends beyond her direct additive genetic effects (Van der Werf, 2002), and can cause the offspring of the same mother to resemble each other (Falconer and Mackay, 1996). When beef producers are choosing a maternal dam line as replacements, it is important to choose an animal that possesses both a good direct additive genetic merit for growth traits as well as maternal effects for milk so she can wean a heavier calf. The linear model pertaining to a maternal effects model is:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z_1a} + \boldsymbol{Z_2m} + \boldsymbol{e}$$

where $\boldsymbol{y}$ is the vector of observations; $\boldsymbol{b}$ is the vector of fixed effects; $\boldsymbol{a}$ is the vector of additive genetic random effects; $\boldsymbol{m}$ is the vector of maternal genetic effects; $\boldsymbol{e}$ is the vector of residual effects; $\boldsymbol{X}$, $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$ are the incidence matrices relating to records of fixed, random effects of the animal (additive genetic) and dam (maternal genetic), respectively (Van der Werf, 2002; Mrode, 2014).

1.3.3.6 Multi-trait model

Traits of interest can be genetically and phenotypically correlated and therefore, to account for such a phenomenon, multiple trait evaluations can be used. By utilising the correlation structure among traits, each trait provides information about all other traits, thus increasing the accuracy of the EBV (Van der Werf, 2002); however, the computational requirements also increases for multi-trait evaluations (Mrode, 2014). Another advantage of multi-trait evaluations is that they are less biased as the models can account for culling selection bias (i.e., when animals are selected to be culled based on the values of a correlated trait) (Mrode, 2014); for instance, the evaluation of second parity dairy cows when culling or selection was based on the first lactation yields (Van der Werf, 2002). Irrespective of whether the animal has an observation for the trait, breeding values will be estimated for each animal and each trait within the analysis (Van der Werf, 2002). The general structure of the multi-trait linear model is:

$$\boldsymbol{y_i} = \boldsymbol{X_i}\boldsymbol{b_i} + \boldsymbol{Z_i}\boldsymbol{a_i} + \boldsymbol{e_i}$$

where $\boldsymbol{y_i}$ is the vector of observations for the *i*th trait; $\boldsymbol{b_i}$ is the vector of fixed effects for the *i*th trait; $\boldsymbol{a_i}$ is the vector of additive genetic random effects for the *i*th trait; $\boldsymbol{e_i}$ is the vector of residual effects for the *i*th trait; $\boldsymbol{X_i}$ and $\boldsymbol{Z_i}$ are the incidence matrices relating to records of fixed, and random effects of the animal (additive genetic) for the *i*th trait, respectively (Van der Werf, 2002; Mrode, 2014).

1.4 Irish Animal Breeding Decision Support Tools

1.4.1 Dairy Decision Support Tools

Two main indexes exist for dairy animals in Ireland, namely the Economic Breeding Index (EBI) for breeding decisions (Berry et al., 2007) and the Cow's Own Worth index (C.O.W.) for culling decisions (Kelleher et al., 2015). Both indexes are routinely published by the Irish Cattle Breeding Federation (ICBF), a non-profit organisation which focuses on providing Irish beef and dairy farmers with DSTs for breeding and selection (ICBF, 2019b).

1.4.1.1 Economic Breeding Index

The EBI is a single-figure profit index decision support tool that aids in the identification of the most profitable bulls and females (based on their additive genetic component) to breed for dairy herd replacements. Prior to the introduction of the EBI in February 2001, the Relative Breeding Index was the selection index available to Irish dairy farmers and was based solely on production traits including milk yield, fat and protein (Berry et al., 2007). Despite the year-on-year improvement in genetic merit for milk yield, fertility merit in the Irish dairy cattle population deteriorated due to the existence of an antagonistic relationship between production and functional traits (Pryce and Veerkamp, 2001). The EBI was established to include both functional and production traits of economic importance within the selection index and was launched in 2001 (Figure 1.6).

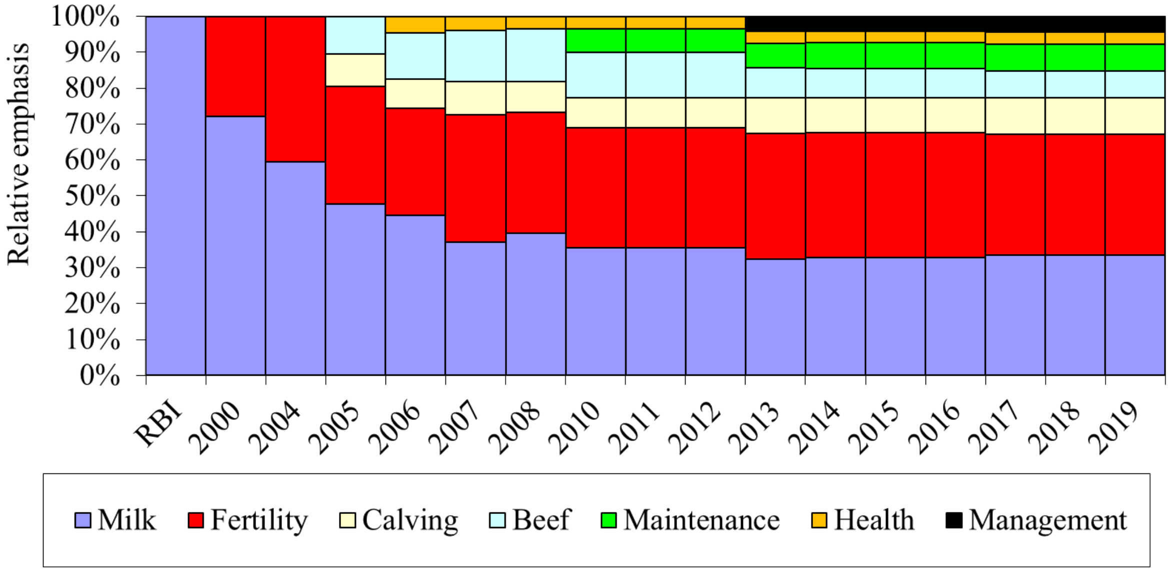

Figure 1.6: The development of the Economic Breeding Index between the years 2000 and 2019.

Genetic evaluations in Ireland are run six times annually and the EBI of each animal is subsequently updated to provide the most up-to-date estimates of genetic merit for farmers when making breeding decisions. Ramsbottom et al. (2006) investigated the validity of the EBI on farm profit using 1,131 dairy herds and reported that there was, in fact, a positive linear relationship between farm net profit and the EBI. Furthermore, it was reported that there was a €1.94 increase in net margin per cow per unit increase in EBI (Ramsbottom et al., 2006). Moreover, the EBI was also positively associated with both the production and fertility sub-indexes, whereby it was reported that for every one unit increase in the corresponding index, the net profit per cow was €3.43 and €1.72, respectively (Ramsbottom et al., 2006). The performance of the Irish national dairy herd has unquestionably improved since the introduction of the EBI and continues to improve. Since 2008, not only has the national calving interval shortened by 9 days, but the percentage of the herd calved in the first 6 weeks of the calving season has also increased by 11%; the number of calves per cow born per year has increased from 0.84 to 0.9 (ICBF, 2019c). The overall change in the profit per lactation for each of the sub-indexes within the EBI over the past 20 years is reported in Figure 1.7.

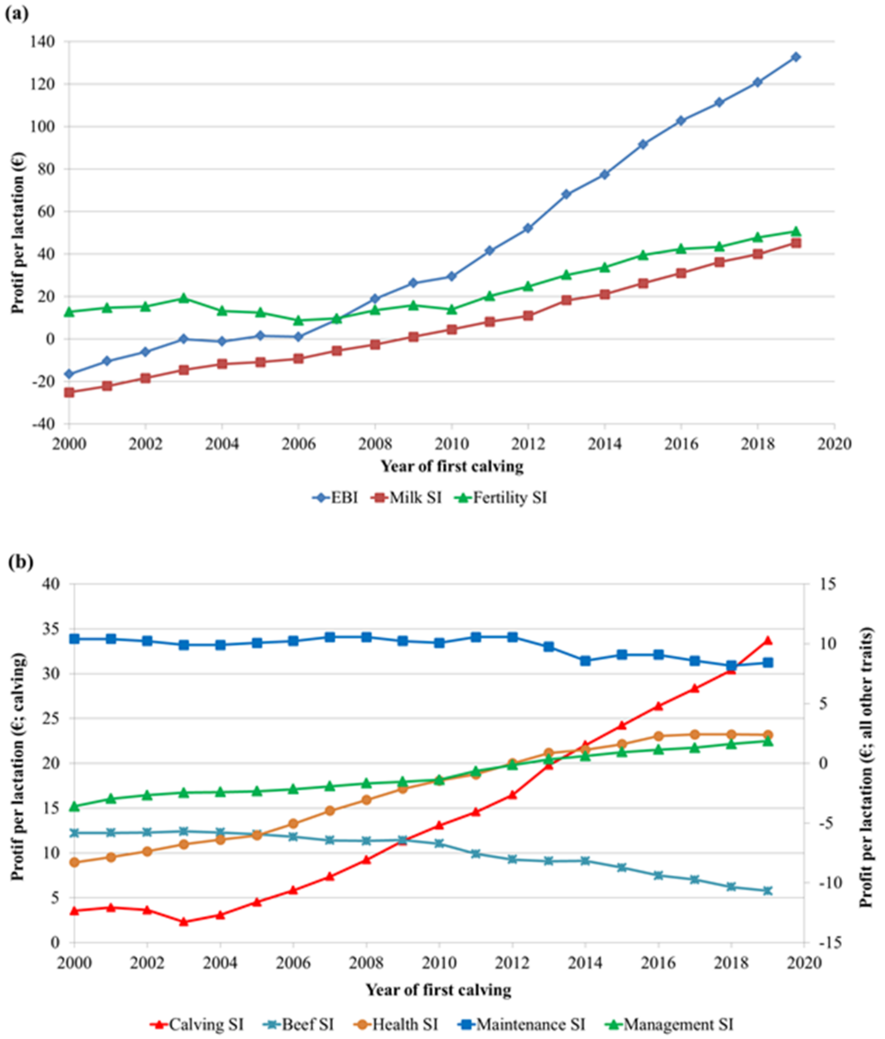

Figure 1.7: Change in profit per lactation over a 20 year period of the (a) Economic Breeding Index value (EBI), milk and fertility sub-indexes (SI) and (b) the five remaining SI within the economic breeding index, namely calving, beef, maintenance, and management SI.

The EBI has been continuously re-evaluated and expanded upon since its introduction and currently comprises of 7 sub-indexes encompassing 19 traits of economic importance (ICBF, 2019g) (Table 1.2).

Table 1.2: Breakdown of sub-indexes, traits, economic weights and overall emphasis of traits within the Economic Breeding Index (ICBF, 2019g).

Sub-Index	Trait	Economic Weight	Overall Emphasis
Production	Milk (kg)	-€0.09	34%
	Fat (kg)	€2.08	
	Protein (kg)	€5.58	
Fertility	Calving interval (d)	-€12.59	34%
	Survival (%)	€12.43	
Calving	Direct calving difficulty (%)	-€4.19	10%
	Maternal calving difficulty (%)	-€2.31	
	Gestation (d)	-€7.93	
	Calf mortality (%)	-€2.58	
Beef	Cow (kg)	€0.15	8%
	Carcass weight (kg)	€1.38	
	Carcass conformation (EUROP)	€10.32	
	Carcass fat (1 to 15 scale)	-€11.71	
Maintenance	Cull cow (kg)	-€1.65	6%
Management	Milking duration (seconds)	-€0.31	5%
	Temperament (units)	€35.86	
Health	Lameness (%)	-€72.47	3%
	Mastitis (%)	-€82.65	
	SCC (Log_e)	-€43.49	

1.4.1.2 Cow's Own Worth

The C.O.W. index is a performance ranking tool for dairy females ranking them based on their predicted profit for the remainder of their lifetime (Kelleher et al., 2015). The C.O.W. index is currently only provided to spring-calving dairy herds as spring-calving systems predominate in Ireland (Berry et al., 2013). Unlike the EBI, the C.O.W. includes not only an estimate of the additive genetic component but also includes the non-additive genetic components as well as environmental effects such as calving date and the age of the cow. The objective of the C.O.W. index is to facilitate the identification of candidate females for culling. Kelleher et al. (2015) developed the C.O.W. model which takes cognisance of the predicted profit from an animal's current lactation and future lactations, as well as the net replacement cost of the animal (Figure 1.8); importantly, by using transition matrices, the expected profit of future lactations includes probability estimates of the dairy cow surviving to subsequent lactations.

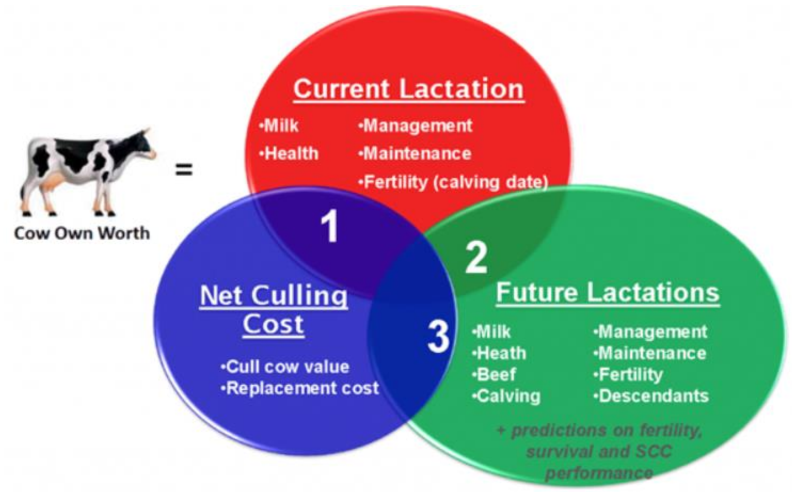

Figure 1.8: Illustration of the sub-components included in the three factors that are used to calculate the Cow's Own Worth value (ICBF, 2019e).

A close relationship exists between the C.O.W. and the EBI with them being viewed as complementary DSTs; because the C.O.W. also incorporates the additive genetic merit of the animal, Kelleher et al. (2015) reported a correlation of 0.65 between the C.O.W. and EBI index. The general objective of all animal breeding programmes tends to be to shift the mean performance of the population in a desired direction. For example, the EBI recommends breeding from the top performing animals on the desirable side of the normal distribution, thus shifting the mean performance in the desirable direction. In contrast, the C.O.W. index recommends culling less profitable animals from the undesirable side of the normal distribution thus shifting the mean performance of the herd further in the desirable direction (Figure 1.9).

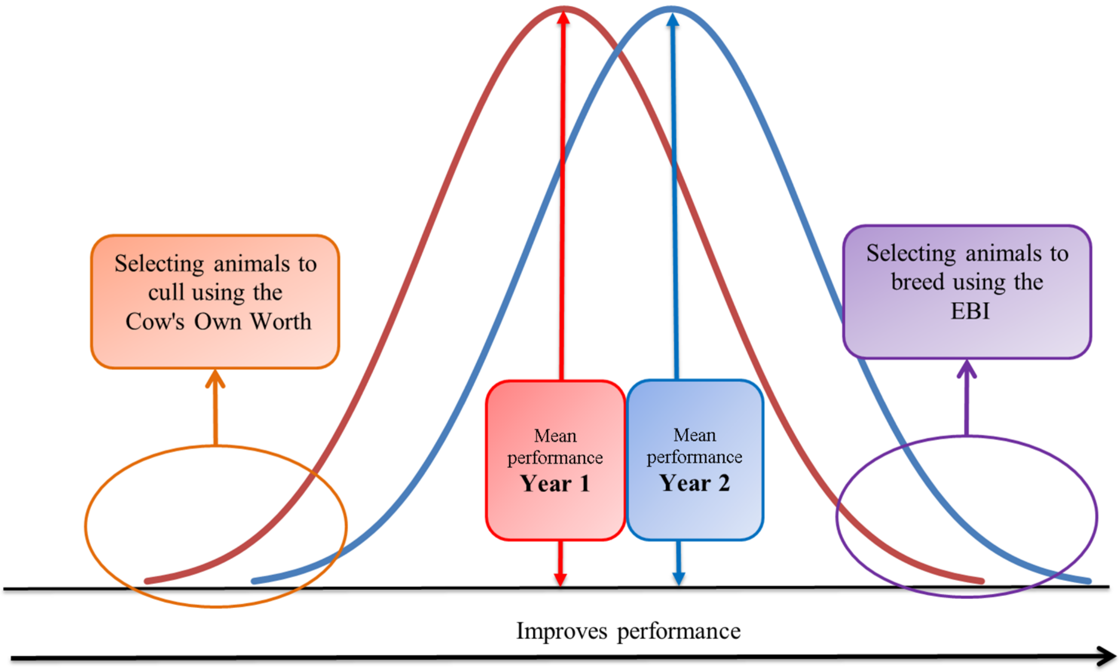

Figure 1.9: Shifting the mean performance of a herd using both the Cow’s Own Worth culling decision support tool and Economic Breeding Index decision support tool.

1.4.2 Beef Decision Support Tools

Two beef breeding indexes exist: 1) the Terminal Beef Index, and 2) the Replacement Index. For ease of identification, animals are reported to have a value of between 1 and 5 stars, representing the bottom performing 20% of animals to the animals performing within the top 20 percentile for a trait, respectively. Both indexes are breeding DSTs and are published 6 times annually by the ICBF.

1.4.2.1 Replacement Beef Index

The Replacement Beef Index is targeted at farmers who wish to select animals that will produce high-profit replacement female progeny. Additive EBVs for both maternal and terminal traits of interest are included in the index (weighted by the economic weights) as the resulting progeny may be kept for breeding or slaughtered (McHugh and McGee, 2016) (Table 1.3).

Table 1.3: A breakdown of the individual components included in the beef replacement index (ICBF, 2017b).

Trait Type	Trait	Economic Weight	Trait Emphasis
Cow Traits (71%)	Maternal calving difficulty (%)	-€4.98	6%
	Age at first calving (d)	-€0.99	6%
	Calving interval (d)	-€5.07	9%
	Survival (%)	€8.86	8%
	Milk (kg)	€5.58	18%
	Heifer intake (kg / DMI)	-€0.76	8%
	Cow intake (kg / DMI)	-€0.55	6%
	Cow docility (1 to 5 score)	€77.27	4%
	Cull cow weight (kg)	€0.91	7%
Calf Traits (29%)	Calving difficulty (%)	-€5.12	7%
	Gestation length (d)	-€2.48	2%
	Mortality (%)	-€5.87	1%
	Docility (1 to 5 score)	€14.72	1%
	Feed intake (kg / DMI)	-€0.07	4%
	Carcass weight (kg)	€2.10	10%
	Carcass conformation (EUROP)	€10.22	3%
	Carcass fat (1 to 15 scale)	-€5.44	1%

1.4.2.2 Terminal Beef Index

The Terminal Beef Index is a breeding DST with the objective of identifying animals that produce the most profitable progeny for slaughter (McHugh and McGee, 2016). The index is comprised of 8 traits including three calving traits (i.e., calving difficulty, gestation length and calf mortality), feed intake, docility and three carcass traits (i.e., carcass weight, carcass conformation and carcass fat) (Table 1.4). Similar to the replacement index, the value given to each animal is estimated based on their additive genetic effect for each trait weighted by the economic importance of the trait.

Table 1.4: A breakdown of the individual components included in the euro-star beef terminal index (ICBF, 2017b).

Trait	Economic Weight	Trait Emphasis
Calving difficulty (%)	-€4.65	18%
Gestation length (d)	-€2.25	4%
Mortality (%)	-€5.34	3%
Docility (1 to 5 scale)	€17.02	2%
Feed intake (kg / DMI)	-€38.63	16%
Carcass weight (kg)	€3.14	41%
Carcass conformation (EUROP)	€14.77	11%
Carcass fat (1 to 15 scale)	-€7.86	5%

1.4.3 The Dairy Beef Index (DBI)

The DBI is a breeding DST that ranks beef bulls on their additive genetic merit for calving traits as well as carcass performance traits, feed intake and docility for their use on dairy females (Berry et al., 2019a). Since the abolition of milk quotas in Ireland in 2015, both dairy herd size and herd numbers have been increasing (Kelly et al., 2017). With this expansion comes the opportunity to use beef bulls on the proportion of dairy cows that are not deemed to have sufficient elite genetic merit and therefore will not be kept as replacements (Berry et al., 2019a). Nevertheless, given the correlated response to selection due to the positive genetic correlation between traits such as calf birth-weight and calving difficulty (Eriksson et al., 2004), there is a necessity to take cognisance of the potential ramifications when mating a beef sire to a dairy dam. Especially given that already the number of beef-sired calves born in dairy herds has been increasing (ICBF, 2017a) (Figure 1.10).

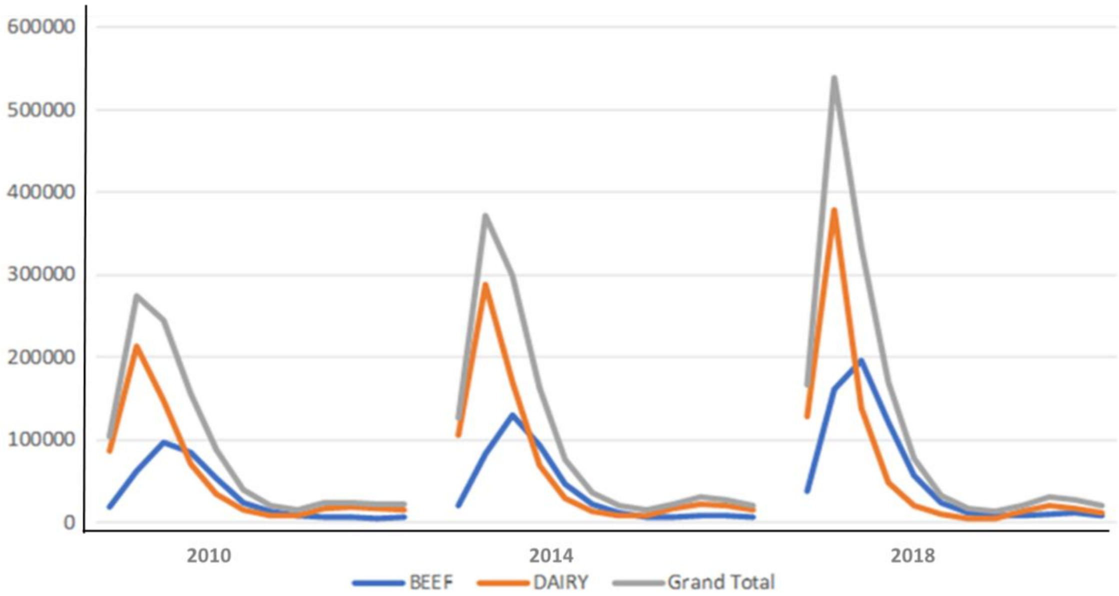

Figure 1.10: Number of calves born from the beef and dairy herd in the years 2010, 2014 and 2018.

Berry et al. (2019a) reported the necessity for developing an index that would rank the suitability of beef bulls being used on dairy dams to ensure two main outcomes: 1) the resulting calf would have a good carcass sales value and, 2) there would be minimal repercussions on the dairy dam with reference to her subsequent fertility and production performance; especially given the positive genetic correlation (r = 0.54) between birth-weight and calving difficulty (Berry et al., 2019a). The overall objective of the DBI is to improve the carcass quality of calves born in the dairy herd thereby increasing the profitability of the calves sold for slaughter (ICBF, 2019f). Similar to the EBI, a single-figure monetary value is calculated for each beef bull which predicts the expected profit from the progeny born to a dairy cow relative to progeny born from a dairy bull. The goal traits within the index vary in relative importance (Figure 1.11). As the index is based on breeding beef sires with dairy dams, calving difficulty is a major factor, and therefore has a 53% trait emphasis within the DBI (ICBF, 2019f).

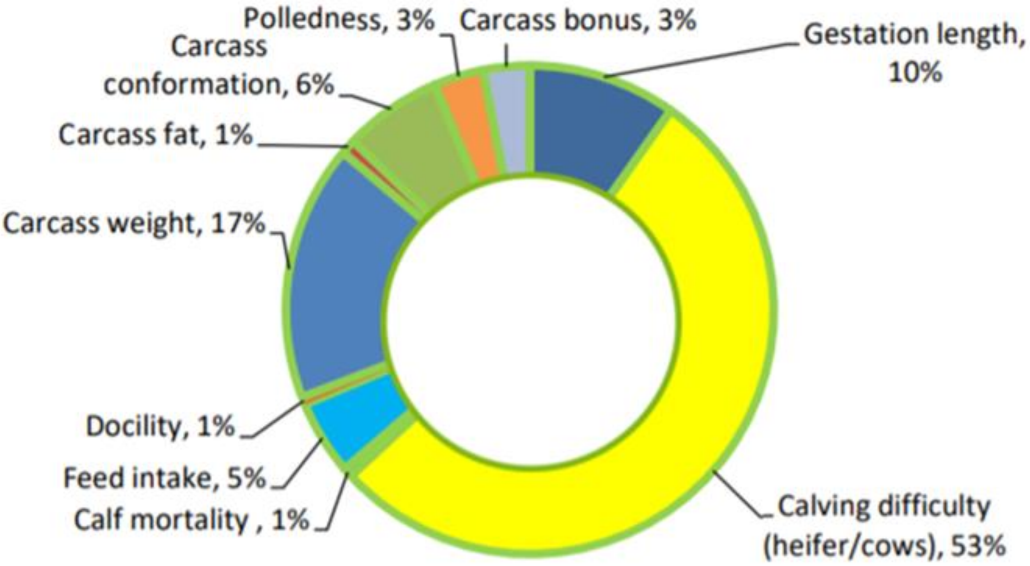

Figure 1.11: A breakdown of the trait emphasis within the dairy beef index (ICBF, 2019f).

A validation study of the DBI was undertaken by Berry and Ring (2020a) whereby the progeny performance of just over 100,000 dairy cows who were mated to either beef or dairy sires were analysed. Progeny born from high DBI beef sires, relative to dairy sires, had superior carcass performance for traits such as weight, conformation as well as a greater proportion of the progeny achieving the overall carcass specifications (Berry and Ring, 2020a). When reporting on the calving performance of the top 20 % of DBI sires, there were increases in perinatal mortality and gestation length relative to dairy sires (Berry and Ring, 2020a); however, dairy sires did have a greater incident of calving difficulty (Berry and Ring, 2020a). Despite this, the expected overall profit from using a high DBI beef sire, relative to a dairy sire, was an additional €44.97 when both calving and carcass performance parameters are accounted for (Berry and Ring, 2020a).

1.5 Gaps in Knowledge

The success of breeding selection indexes around the world has been well documented in the literature (Berry et al., 2007; McHugh et al., 2014; Cole and VanRaden, 2018). The incorporation of best linear unbiased predictions within the decision-support tools has been the foundation of such success. Best linear unbiased estimations (BLUEs) have, however, been largely ignored. BLUEs have a huge potential role in DSS as they can scientifically quantify the management and environmental effects of each herd independent of the herd's mean genetic merit. Furthermore, a fundamental assumption of genetic evaluations is that a one unit change in breeding value equates to a one unit change in phenotypic performance in the average herd; however the phenotypic change in response to changes in EBVs in a well-managed herd or in a poorly managed herd, may differ from this expectation. As BLUEs can be used to categorise the status of the management a herd is operated under, BLUEs have the potential to serve as an indicator of the expected response to selection, especially at key decision points (e.g. purple boxes indicated in Figure 1.12.) prior to bull selection. This would enable advisors to adapt and tailor breeding strategies for each individual farm based on the expected future performance.

Irish selection indexes for beef animals have primarily focused on supporting breeding decisions which assist in the identification of genetically superior parents who will produce the next generation. Furthermore, beef selection indexes only take cognisance of additive genetic effects and therefore ignore non-additive and non-genetic effects which can impact the performance potential of an animal. Voids do exist in the beef DST repertoire. Currently there is no form of guidance available to producers who wish trade growing cattle for a monetary value reflective of their eventual harvest value. Nor is there an index available which is capable of ranking beef females based on their expected lifetime performance potential, to assist in the selection of candidate females both either retention or culling from the herd. Coupled with the fact that neither of the proposed DSTs are for breeding purposes, the opportunity to include both non-additive and non-genetic effects into the estimation of such indexes also exists. Figure 1.12 portrays both the Irish dairy and beef DSTs available, identifies voids in decision support within both sectors, and illustrates where DSTs could be shared between both sectors.

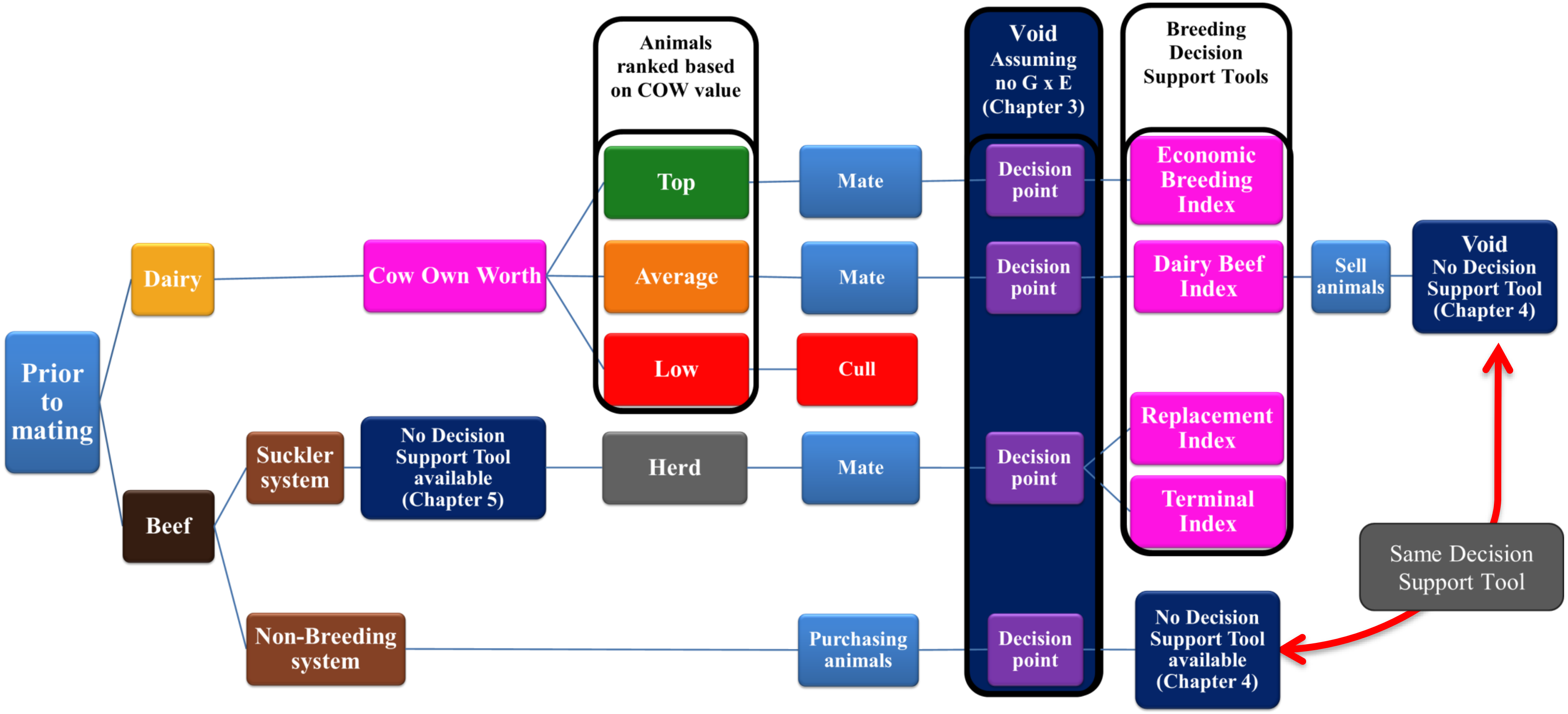

Figure 1.12: An integrated decision tree for both Irish dairy and beef enterprises indicating which decision support tools (pink boxes) are useful at various production time-points (light blue boxes). The voids in decision support tools are also identified by the navy blue boxes. The assumption that there is no genotype by environment interaction (G × E) at the decision points when bulls are chosen for breeding the future progeny within the dairy and beef cow system, as well as within the non-breeding beef system whereby animals are assumed to perform equally across environments.

Chapter 2:

Characterisation of best linear unbiased estimates generated from national genetic evaluations of reproductive performance, survival, and milk yield in dairy cows

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Formatting and referencing style has been edited for consistence throughout the thesis. Figures and tables have also been edited to conform to the thesis. All other aspects are consistent with the published manuscript.

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2.1 Abstract

Genetic evaluations decompose an observed phenotype into its genetic and non-genetic components; the former are termed best linear unbiased predictions (BLUPs) with the solutions for the systematic environmental effects in the statistical model termed best linear unbiased estimates (BLUEs). Geneticists predominantly focus on the BLUPs and rarely consider the BLUEs. The objective of this study, however, was to define and quantify the association between eight herd-level characteristics and BLUEs for six traits in dairy herds namely 1) age at first calving, 2) calving to first service interval (CFS), 3) number of services, 4) calving interval (CIV), 5) survival, and 6) milk yield. Phenotypic data along with the fixed and random effects solutions were generated from the Irish national multi-breed dairy cow fertility genetic evaluations on 3,445,557 cows; BLUEs for individual contemporary groups were collapsed into mean herd-year estimates. Data from 5,707 spring-calving herds between the years 2007 and 2016 inclusive were retained; association analyses were undertaken using linear mixed multiple regression models. Pearson coefficient correlations were used to quantify the relationships among individual trait herd-year BLUEs and transition matrices were used to understand the dynamics of mean herd BLUE estimates over years. Based on the mean annual trends in raw, BLUPs, and BLUEs, it was estimated that BLUEs were associated with at least two thirds of the improvement in CIV and milk production over the past ten years. Milk recording herds calved heifers for the first time on average 15 d younger, had an almost 2 d longer CFS but 2.3 d shorter CIV than non-milk recording herds. Larger herd sizes were associated with worse BLUEs for both CFS and CIV. Expanding herds and herds that had the highest proportion of cows born on the farm itself, on average, calved heifers younger and had shorter CIV. By separating the raw performance of a selection of herds into their respective BLUEs and BLUPs, it was possible to identify herds with inferior management practices that were being compensated by superior genetics; similarly, herds were identified with superior BLUEs, but because of their inferior genetic merit, were not reaching their full potential. This suggests that BLUEs could have a pivotal role in a tailored decision support tool that would enable producers to focus on the most limiting factor hindering them achieving their maximum performance.

2.2 Introduction

Animal breeders have traditionally focused on improving the mean genetic merit of a population in the pursuit of enhanced performance. Animal performance, however, is a function of both the genotype of the animal and the environment it is (and was) exposed to. Failure to improve animal management concomitant with the requirements of the genetically elite germplasm, hampers the actual realisation of the benefit in genetic gain. Genetic evaluations apportion the phenotype of an individual into its estimated additive genetic merit (i.e., Best Linear Unbiased Predictions; BLUPs) and the contributing environmental or management influences (i.e., Best Linear Unbiased Estimates; BLUEs). While the BLUPs have been extensively used in animal breeding programs (Meuwissen et al., 2001; Muir, 2007; Patry and Ducrocq, 2011), BLUEs have received considerably less attention. Most genetic evaluations consider as fixed effects some measure of temporal herd groupings such as the contemporary group of herd-year-season (van Bebber et al., 1997; Calus et al., 2005) or just herd-year (Englishby et al., 2017). Bastin et al. (2009) proposed using such herd-year BLUEs to provide dairy producers with retrospective advice on feeding and management strategies. Bastin et al. (2009) found that by analysing the BLUEs associated with the milk urea concentration of milk samples, an association could be made between dietary crude protein and the dietary management of the animals. This information could then be used to provide farmers with on-going feed management advice (Bastin et al., 2009). Similarly, Caccamo et al. (2008) included a herd-test-day effect in the statistical analyses of dairy cow milk performance data to account for short term management changes such as changes in feed ration. Englishby et al. (2017) used BLUEs to independently quantify the association between management environments and the variability in beef carcass characteristics after accounting for differences in additive genetic merit; Englishby et al. (2017) achieved this by including the random effects of both animal genetic merit and the contemporary group of finishing herd-year in the statistical model. Studies are however lacking, in dairy cattle at least, on the macro-environmental and management characteristics describing the BLUEs. The objective of the present study was to describe herd-level related factors contributing to herd-year BLUEs and to understand the inter-relationships among herd-year BLUEs for fertility, milk and survival in dairy cows. The information generated has the potential to be used within a management decision support tool to enable producers make more informed value-creating decisions.

2.3 Materials and Methods

All data used in the present study originated from the Irish Cattle Breeding Federation (ICBF) database, Bandon, Co. Cork, Ireland.

2.3.1 Genetic Evaluation

The edited phenotypes and associated fixed effects used in the Irish national multi-breed dairy cow fertility genetic evaluations were available; data on a total of 3,445,557 cows were available which consisted of predominantly Holstein-Friesian (91%) with the remainder being mainly crossbred animals. A national genetic evaluation was subsequently run in MiX99 (MiX99 Development Team, 2015) and the fixed effects (and random effects) solutions generated. The national dairy cow fertility genetic evaluation used in Ireland is a 23 × 23 multi-trait evaluation which includes age at first calving, calving to first service interval from parity 1 to 3 as separate traits, number of services from parity 1 to 3 as separate traits, calving interval from parity 1 to 5 as separate traits, 305-day milk yield from parity 1 to 5 as separate traits, survival from parity 1 to 5 as separate traits, and lifespan; lifespan was not considered further. Details of the editing procedures, statistical models and variance components for each trait are described in Berry et al. (2013). Fixed effects common to all traits were the contemporary group of herd-year-season of calving (or birth when the dependent variable was age at first calving), age at calving (except when the dependent variable was age at first calving), heterosis and recombination loss coefficients. Contemporary groups are created for each trait using the procedure outlined in Berry et al. (2013) based on algorithms proposed by Crump et al. (1997) and Schmitz et al. (1991).

2.3.2 Definition of Herd-Year BLUE effects

Contemporary group BLUEs from the national genetic evaluations were available. Contemporary group effect estimates were not necessarily available for all traits; for example herds that do not participate in milk recording would not have a contemporary group effect estimate for 305-d milk yield but could have a contemporary group effect estimate for any of the fertility traits. A given herd-year could have several contemporary groups because clusters of animals may calve at different periods of the year within a herd and therefore would be in different contemporary groups; therefore the average contemporary group effect estimate within each herd-year, weighted by the respective number of records in each contemporary group, was calculated. Only data from herds with information for each year in the 10-yr period from 2007 to 2016 inclusive were retained; annual herd-year BLUEs for each of the 10 yrs were available from 8,873 herds (i.e., 88,730 herd-years).

2.3.3 Herd-Year level characteristics

Herd-year characteristics of interest included: 1) geographical location, 2) whether or not the herd was milk recording, 3) herd size, 4) herd expansion rate, 5) herd-level use of AI, 6) the proportion of cows in the herd that were born in that herd (i.e., not purchased), 7) the proportion of cows in the herd that were registered with a breed society, and 8) the proportion of cows in the herd that calved in the first 42 days of the calving season (Calv42). Geographical location was available for all herds in the Republic of Ireland on a county basis; herds originated from a total of 26 counties with the three largest counties in the country further subdivided into north and south. A herd was defined as a milk recording herd in a given year based on the presence of milk recording data for that herd in the national database for that year; all data from milk recorded herds are stored in the central database.

Herd size for a given herd-year was based on the number of calving events in that year. The trend in annual herd size was used to calculate the rate of expansion using an approach similar to that described in detail by Jago and Berry (2011); a linear robust regression was used to calculate the expansion rate of each herd-year from 2007 to 2016 inclusive. To calculate the rate of expansion for a given year, the herd size of that year as well as the two flanking years were used in the robust regression; the exception were the years 2007 and 2008 as well as 2015 and 2016 but in these cases, 5 years' data were always included. The resulting linear coefficient was used to categorise the rate of herd expansion as outlined in Jago and Berry (2011); herds deemed not to be expanding were those with a negative linear regression coefficient or a linear regression coefficient not different (i.e., $P > 0.05$) from zero.

The extent of AI usage in a given herd-year was calculated as the proportion of cows that calved in that herd-year that had received at least one AI in that year. In Ireland it is a legal requirement to register all bovine birth events including the herd of birth; the proportion of cows calving in a herd in a given year that were actually born in that herd was therefore available. Similarly, the proportion of cows calving in a given herd-year that were registered with a breed society was also generated.

Irish dairy herds are typically seasonal calving with the majority of cows calving in a short number of months in the spring (Berry et al., 2013); the start of the spring calving season in a given herd was characterised by a minimum of five cows calving within a 14-d period (Berry et al., 2013). Similar to Berry et al. (2013), the proportion of calving events within the first 42 d of the calving season relative to the number of cows that calved that year was calculated per herd-year.

2.3.4 Data editing and categorisation of herd characteristic variables

Only herds that had ≥30 calving events in all 10 yrs (5,707 herds) were retained. Furthermore, only spring-calving herds, which predominate in Ireland (Berry et al., 2013); were retained; in 2016, 86 % of calves born to a dairy sire were born during the months January to April, inclusive (DAFM, 2016). A spring-calving herd was defined as a herd where at least 80% of calving events occurred between January and June, inclusive. For the analysis of herd characteristics, a single herd-year BLUE for each of the five traits that contained multiple parities (i.e., calving to first service interval, calving interval, number of services, milk yield, and survival) was calculated as the weighted (by number of records per parity) average across all three (i.e., calving to first service interval and number of services) or five (i.e., calving interval, milk yield, and survival) parities. Only average herd-year BLUEs for calving interval, milk yield and survival were retained if a herd-year BLUE was available for at least 4 of the parities each containing a minimum of five records; average BLUEs for calving to first service interval and number of services required herd-year BLUEs to be available for at least 2 parities with a minimum of five records per parity. The mean herd-year BLUE of each collapsed trait was subsequently recoded to be relative to the mean of the entire population.

Each of the herd-level characteristics, with the exception of geographical location and milk recording, were stratified into five categories; as contemporary group effects were not available for all traits, in order to accurately represent the population distribution for herd size and the proportion of AI used on farm, the threshold values categorising each characteristic varied per BLUE (Supplementary Table S2.1). Transition matrices were generated to investigate the dynamics of herd BLUEs between adjacent years. Herd-year BLUEs for each trait were stratified separately into five strata of equal size based on the annual herd performance for each individual trait and subsequently averaged across years; the first strata represented the top performing herd-year BLUEs for each trait and the fifth strata represented the worst performing herd-year BLUEs. For example, the highest milk yielding herd-year BLUEs were represented in stratum 1, whereas stratum 5 represented the lowest milk yielding herd-year BLUEs; similarly the shortest BLUE for calving interval was represented in stratum 1 and the longest BLUE for calving interval was in stratum 5. Transition matrices between adjacent years were generated and averaged.

2.3.5 Statistical analyses

Pearson coefficient correlations were used to estimate the inter- and intra-relationships between parity-specific BLUEs for all traits. Correlations among all traits at an individual parity level were estimated for each year separately, and subsequently averaged across years; similarly, correlations between the single herd-year BLUEs were estimated for each year separately and then averaged across years. The association between each herd-level characteristic and each of the six averaged BLUEs (i.e., age at first calving, calving to first service interval, calving interval, number of services, survival, and milk yield) was quantified using a linear mixed multiple regression model in SAS 9.4 software (SAS Institute Inc., Cary, NC), where the dependent variable was the herd-year average BLUE. The fixed effects in the model were those describing the herd characteristics; year was forced into all models. Herd was included as a repeated effect with the appropriate covariance structures assumed among repeated records; the most appropriate covariance structure was based on the Akaike’s information criterion (Bozdogan, 2000). The repeatability for each BLUE was also estimated from the mixed model. The transition matrices were used to quantify the probability of a herd remaining or changing BLUE category between adjacent years for each of the six traits investigated.

2.4 Results

2.4.1 Correlations

Calving to first service interval BLUEs between parities one to three were weakly correlated with each other (0.31 to 0.39; SE = 0.006; $P < 0.001$). The correlation between number of services BLUEs across the first three parities ranged from 0.46 (between parity one and three) to 0.49 (between parity one and two) (SE = 0.006; $P < 0.001$). Calving interval BLUEs between the first five parities were weakly correlated (0.13 to 0.26; SE = 0.005 to 0.006; $P < 0.001$) with each other. Survival BLUEs were weakly correlated (0.11 to 0.21; SE = 0.005 to 0.006; $P < 0.001$) among parities one to five. Strong correlations existed between milk yield BLUEs in each of the five parities varying from 0.81 (between parity one and five) to 0.90 (between parity two and three) (SE = 0.006 to 0.007; $P < 0.001$). Weak correlations existed between BLUEs of different traits, within the same parity, ranging from -0.17 (between CFS and NS, in parity 2; SE =0.006; $P < 0.001$) to 0.34 (between NS and CIV, in parity 1; SE = 0.006; $P < 0.001$) (Table 2.1). The single parity BLUEs that were collapsed into individual mean BLUEs were weakly correlated with each other ranging from -0.18 (between CFS and NS; SE = 0.006; $P < 0.001$) to 0.31 (between NS and CIV; SE = 0.008; $P < 0.001$) (Table 2.2).

2.4.2 Annual best linear unbiased estimate trends

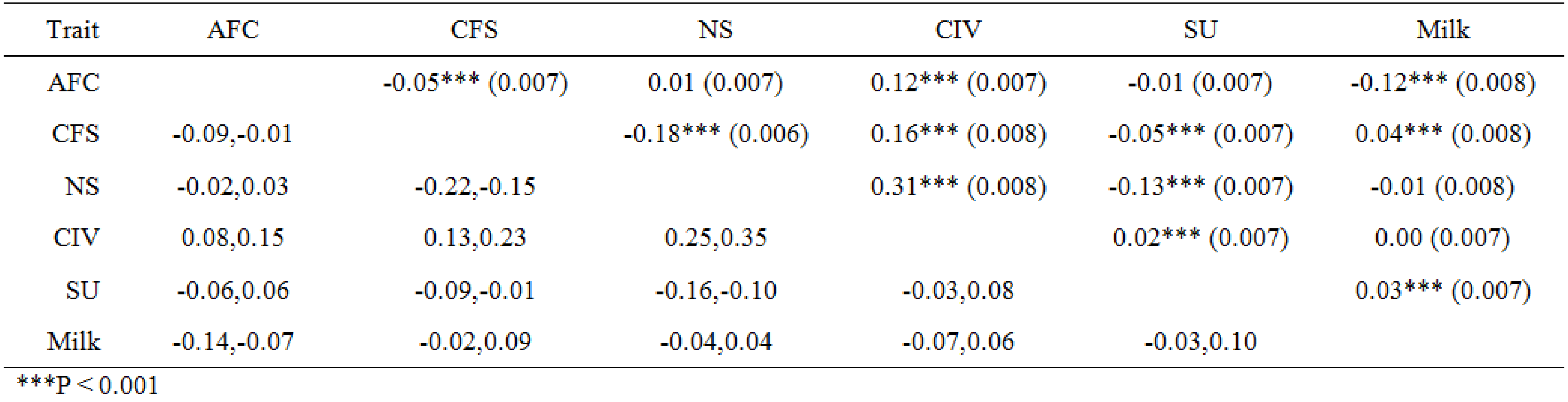
Mean annual BLUE for age at first calving spiked in length twice (i.e., in 2008 and 2012) to approximately 13 d on both occasions and then fell to -6.7 d in 2014 (Figure 2.1). The mean annual BLUE for calving to first service interval lengthened between the years 2007 to 2009 and peaked in the year 2013 (2.9 d); after a sharp fall to -1.1 d in 2014, the mean annual BLUE for calving to first service interval began to lengthen again (Figure 2.1). Mean annual BLUE for number of services reduced between the years 2007 and 2015 resulting in a difference of 0.13 services (from 0.05 to -0.07 serves); during the same period of time, calving interval BLUE shortened by 6.9 d (Figure 2.1). Mean annual BLUE for survival reduced from 2007 to 2013 (Figure 2.1), after which it began to improve. After a reduction in mean annual BLUE for milk yield from 126 kg in 2007 to -391 kg in 2009, mean annual BLUE for milk yield increased to 207 kg in 2015 (Figure 2.1).

Table 2.1: Within parity correlations (standard errors in parentheses) between annual herd-year best linear unbiased estimates for calving to first service interval (CFS), number of services (NS), calving interval (CIV), survival (SU) and milk, averaged across the years 2007 to 2016; with the exception of age at first calving (AFC), which were averaged across the years 2007 to 2014.

		Parity				
Main Trait	Sub Trait	1	2	3	4	5
AFC	CFS	-0.07*** (0.007)	-0.03*** (0.007)	0.00 (0.007)		
	NS	0.00 (0.007)	0.02* (0.007)	-0.01 (0.007)		
	CIV	0.10*** (0.005)	0.09*** (0.005)	0.07*** (0.006)	0.09*** (0.006)	0.03*** (0.007)
	SU	0.02*** (0.005)	0.01 (0.005)	0.02*** (0.006)	-0.03*** (0.006)	0.02** (0.006)
	Milk	-0.10*** (0.007)	-0.14*** (0.007)	-0.13*** (0.007)	-0.14*** (0.007)	-0.14*** (0.007)
CFS	NS	-0.11*** (0.006)	-0.17*** (0.006)	-0.17*** (0.006)		
	CIV	0.23*** (0.006)	0.20*** (0.006)	0.19*** (0.006)		
	SU	-0.03*** (0.006)	-0.01** (0.006)	-0.02*** (0.006)		
	Milk	0.07*** (0.007)	0.05*** (0.007)	0.07*** (0.007)		
NS	CIV	0.34*** (0.006)	0.34*** (0.006)	0.31*** (0.006)		
	SU	-0.16*** (0.006)	-0.14*** (0.006)	-0.14*** (0.006)		
	Milk	-0.01 (0.007)	0.01 (0.007)	0.02*** (0.007)		
CIV	SU	0.03*** (0.005)	0.01 (0.005)	0.05*** (0.005)	0.04*** (0.005)	0.16*** (0.006)
	Milk	0.00 (0.006)	0.01* (0.006)	0.05*** (0.006)	0.05*** (0.006)	0.06*** (0.007)
SU	Milk	0.03*** (0.006)	0.04*** (0.006)	0.01* (0.006)	0.03*** (0.006)	0.01 (0.006)

*P < 0.05, **P < 0.01, ***P < 0.001

Table 2.2: Average correlations (standard errors in parentheses) across years (above diagonal) as well as the minimum and maximum correlations for any given year (below diagonal) between individual herd-year BLUEs.



Trait	AFC	CFS	NS	CIV	SU	Milk
AFC		-0.05*** (0.007)	0.01 (0.007)	0.12*** (0.007)	-0.01 (0.007)	-0.12*** (0.008)
CFS	-0.09,-0.01		-0.18*** (0.006)	0.16*** (0.008)	-0.05*** (0.007)	0.04*** (0.008)
NS	-0.02,0.03	-0.22,-0.15		0.31*** (0.008)	-0.13*** (0.007)	-0.01 (0.008)
CIV	0.08,0.15	0.13,0.23	0.25,0.35		0.02*** (0.007)	0.00 (0.007)
SU	-0.06,0.06	-0.09,-0.01	-0.16,-0.10	-0.03,0.08		0.03*** (0.007)
Milk	-0.14,-0.07	-0.02,0.09	-0.04,0.04	-0.07,0.06	-0.03,0.10	

***P < 0.001

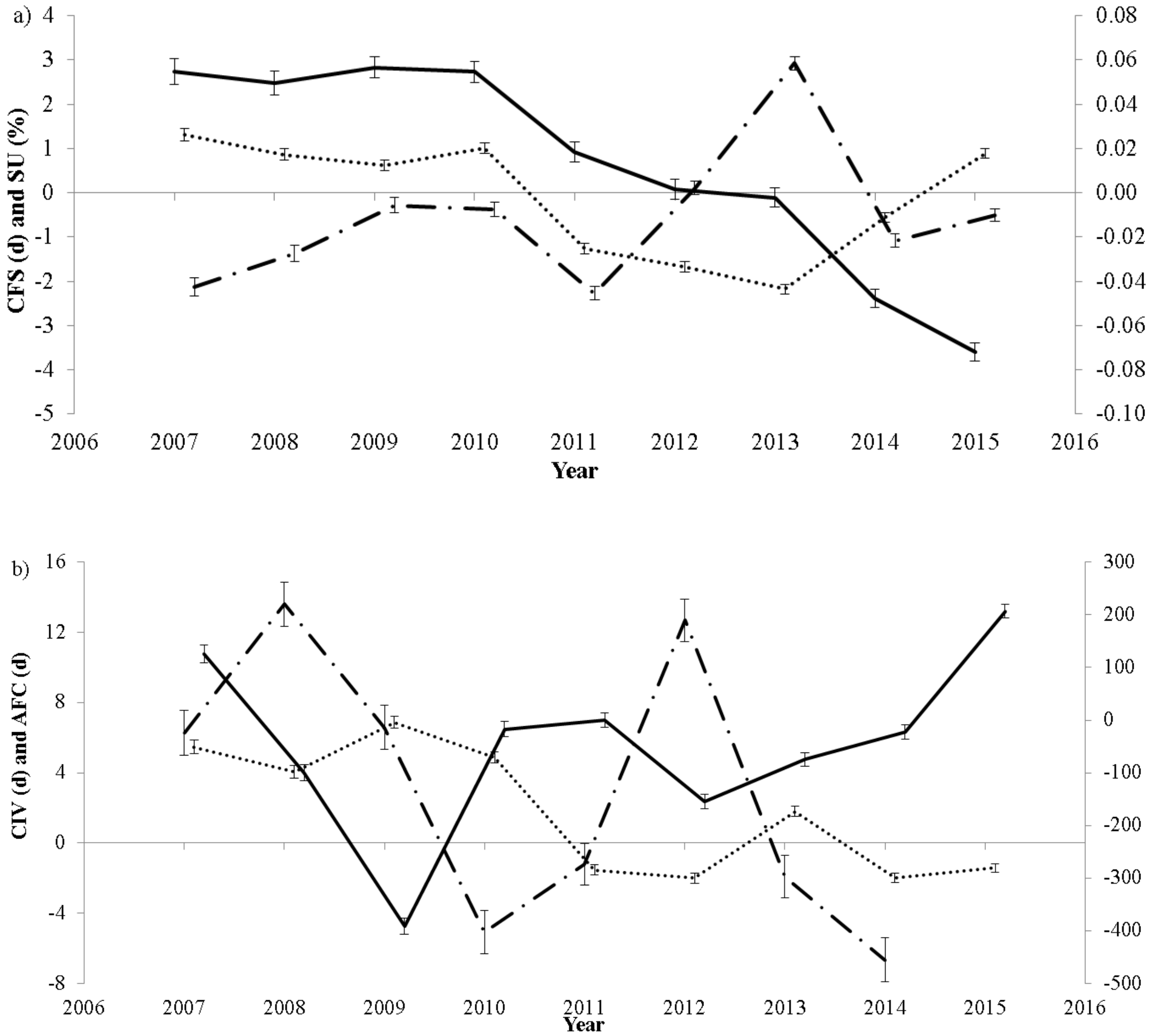


Figure 2.1: Annual least squares means (one standard error each side represented as error bars) of the best linear unbiased estimates for a) survival (SU; ···), calving to first service (CFS; — · —), and number of services (NS ;——), and b) calving interval (CIV; ···), age at first calving (AFC; — · —) and milk yield (Milk ;——).

2.4.3 Repeatability and Transition Matrices

The repeatability of herd-year BLUE for both age at first calving (0.49) and number of services (0.35) across years was moderate; the mean BLUEs for calving to first service interval, calving interval and survival across years were, however, lowly repeatable, ranging from 0.20 to 0.28. The mean BLUE for milk yield across years was highly repeatable at 0.74. Based on the transition matrices between consecutive years (Table2.3; SE ranged from 0.11 to 2.08), there was generally a greater probability for herds to remain within the same stratum from one year to the next. The probability of transitioning to an alternative stratum reduced as the distance between strata compared increased. For example, herds in the stratum representing the highest yielding mean BLUE for milk had a 74% probability of remaining in that stratum the following year but only a 0.42% probability of transitioning to the lowest yielding stratum; herds in the lowest milk yielding stratum had a 69% probability of remaining in that stratum the following year and a 0.43% probability of transitioning to the highest yielding stratum the subsequent year (Supplementary Figure S9.1). A sensitivity analysis was conducted by increasing the number of strata used to characterise the herd-year BLUEs. However, the same phenomenon reoccurred whereby the probability of transitioning into an alternative stratum decreased as the distance between the strata increased.

Table 2.3: Transition matrices between consecutive years for herd-level best linear unbiased estimate strata for each trait (standard errors in parentheses).

	Transition state				
Initial state	1	2	3	4	5
Age at first calving					
1	36.97 (0.43)	25.43 (0.49)	18.06 (0.53)	12.51 (0.49)	07.03 (0.34)
2	23.74 (0.70)	28.87 (0.53)	23.99 (0.37)	16.08 (0.76)	07.32 (0.59)
3	18.64 (0.29)	22.82 (0.40)	25.58 (0.54)	22.64 (0.34)	10.32 (0.84)
4	14.15 (0.34)	15.62 (0.50)	21.63 (0.76)	28.77 (0.81)	19.82 (1.09)
5	07.40 (0.98)	07.53 (0.70)	11.17 (0.60)	19.75 (0.35)	54.15 (2.08)
Calving to first service interval					
1	36.39 (1.16)	22.85 (0.68)	17.34 (0.68)	13.24 (0.98)	10.19 (0.49)
2	19.90 (0.61)	24.24 (0.61)	22.29 (0.48)	19.47 (0.27)	14.10 (0.31)
3	13.24 (0.49)	21.00 (0.63)	21.98 (0.52)	24.22 (0.49)	19.56 (0.49)
4	11.56 (0.70)	17.12 (0.70)	23.41 (0.78)	25.61 (0.26)	22.30 (0.56)
5	10.85 (0.57)	14.29 (0.49)	19.61 (0.65)	22.87 (0.45)	32.38 (1.04)
Number of services					
1	46.68 (1.04)	26.05 (0.80)	13.63 (1.06)	07.95 (0.56)	05.69 (0.41)
2	21.44 (0.67)	29.45 (0.53)	24.45 (0.63)	16.10 (0.74)	08.56 (0.51)
3	10.85 (0.48)	22.17 (0.50)	27.03 (0.48)	24.69 (0.27)	15.25 (0.36)
4	06.73 (0.29)	14.48 (0.64)	23.37 (0.79)	28.99 (0.76)	26.44 (0.68)
5	03.14 (0.23)	07.54 (0.46)	14.37 (0.63)	26.73 (0.62)	48.22 (0.51)
Calving interval					
1	26.07 (0.82)	25.16 (0.81)	21.83 (0.73)	17.33 (0.70)	09.62 (0.37)
2	22.33 (0.87)	25.47 (0.63)	22.10 (0.78)	18.83 (0.65)	11.28 (0.33)
3	20.60 (0.35)	22.15 (0.92)	22.55 (0.67)	20.02 (0.65)	14.68 (0.37)
4	16.86 (0.83)	16.97 (0.33)	21.14 (0.51)	23.57 (0.26)	21.47 (0.53)
5	11.30 (0.71)	11.83 (0.69)	15.81 (0.62)	21.43 (1.04)	39.64 (0.86)
Survival					
1	37.27 (0.71)	22.72 (0.63)	16.81 (0.45)	13.95 (0.39)	09.26 (0.53)
2	21.31 (0.57)	23.83 (0.67)	22.00 (0.30)	18.28 (1.02)	14.57 (0.42)
3	15.49 (0.41)	21.62 (0.46)	22.06 (0.50)	22.18 (0.57)	18.65 (0.42)
4	12.12 (0.31)	19.25 (0.42)	21.58 (0.53)	24.34 (0.35)	22.72 (0.47)
5	07.74 (0.46)	13.34 (0.45)	19.13 (0.76)	24.48 (0.47)	35.30 (0.60)
Milk yield					
1	73.95 (0.47)	19.94 (0.75)	04.62 (0.56)	01.08 (0.13)	00.42 (0.14)
2	21.15 (0.90)	46.12 (0.81)	24.21 (0.69)	07.36 (0.42)	01.15 (0.11)
3	04.50 (0.33)	25.35 (0.53)	40.34 (0.51)	25.15 (0.59)	04.66 (0.37)
4	00.71 (0.14)	08.18 (0.51)	25.14 (0.99)	42.60 (0.83)	23.37 (0.71)
5	00.43 (0.11)	01.28 (0.19)	06.21 (0.46)	22.71 (0.61)	69.38 (0.86)

2.4.1 Herd Level Characteristics

Least square means for age at first calving BLUE varied from -12.5 d to 46 d depending on geographical location while mean BLUE for calving to first service interval differed across geographical location by 5.2 d. Least square means for number of services BLUEs ranged from -0.06 to 0.13 depending on geographical location. A difference of 12.8 d for mean calving interval BLUE, 7.3% for mean BLUE for survival and, 2,280 kg for mean BLUE for milk yield existed when comparing the respective extreme geographical locations. Milk recording herds calved heifers for the first time on average 15 d younger, had a calving to first service interval that was almost 2 d longer and a calving interval that was 2.3 d shorter compared to herds that did not milk record; however minimal difference in number of services (0.01 serves) and survival (0.4%) existed depending on whether or not the herd milk recorded.

A younger mean BLUE for age at first calving was associated with larger herds and herds that expanded at a faster rate. A similar trend was found in herds that used a greater proportion of AI and had a greater proportion of calves born on the farm. There was a tendency for herds that had a greater proportion of cows calving in the first 42 days of the calving season as well as an increased proportion of cows that were registered with a breed society to also be associated with a younger mean BLUE for age at first calving (Figure 2.2).

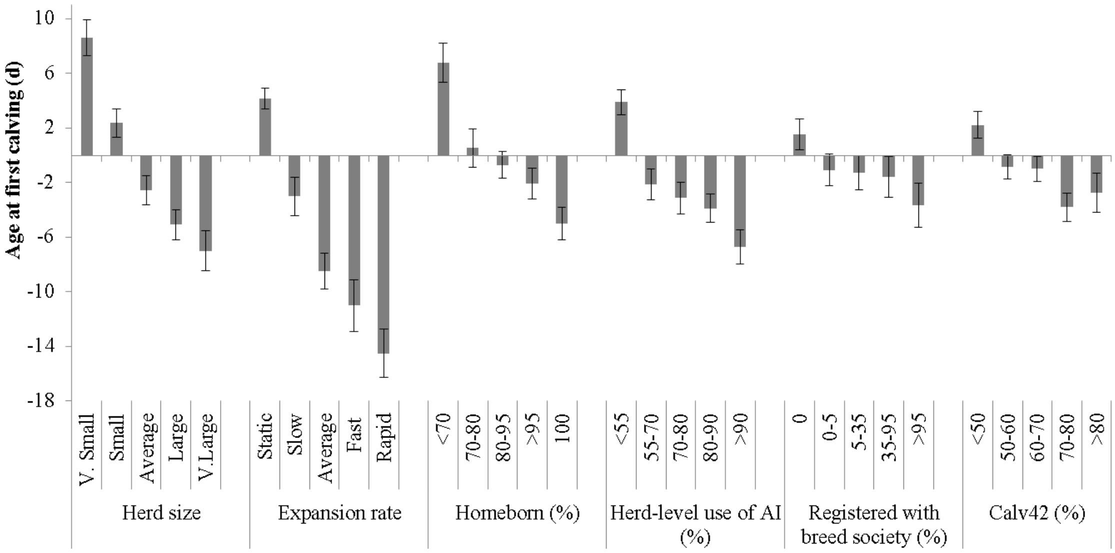


Figure 2.2: Mean (one standard error each side represented as error bars) best linear unbiased estimate for age at first calving for each category of six herd-level characteristics.

A longer mean BLUE for calving to first service interval was associated with larger herd size and a faster expansion rate, as well as being associated with a greater proportion of animals born on the farm, a greater proportion of cows registered with a breed society and a greater proportion of cows that calved in the first 42 d of the calving season. A reduction in the proportion of AI used on farm was associated with a longer mean BLUE for calving to first service interval (Figure 2.3).

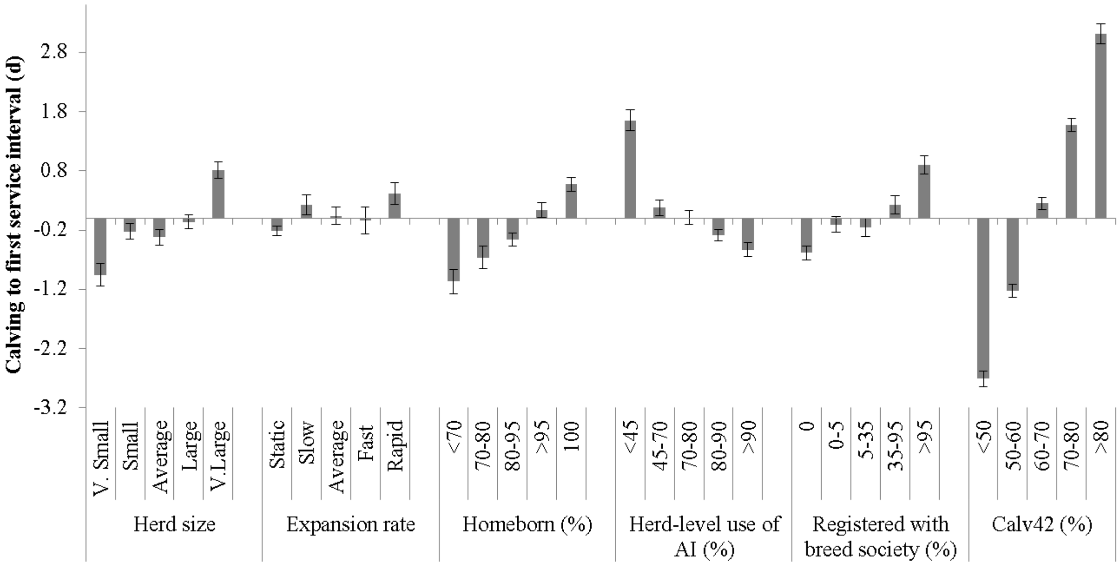


Figure 2.3: Mean (one standard error each side represented as error bars) best linear unbiased estimate for calving to first service interval for each category of six herd-level characteristics.

Very little variability existed in the mean BLUE for number of services across different herd sizes, expansion rates and the proportion of animals born onto the farm. There was a tendency for mean BLUE for number of services to increase in association with increases in the proportion of AI used on farm and the proportion of animals registered with a breed society as well as a decrease in the proportion of cows calved within the first 42 d of the calving season (Figure 2.4).

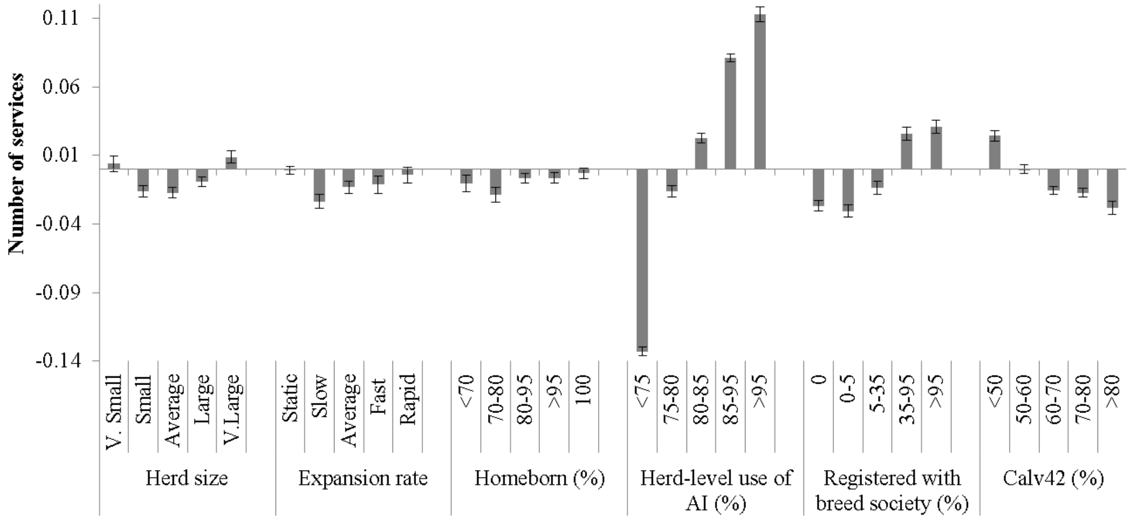


Figure 2.4: Mean (one standard error each side represented as error bars) best linear unbiased estimate for number of services for each category of six herd-level characteristics.

Longer mean BLUEs for calving interval were associated with larger herds, herds that were not expanding, herds that purchased a greater proportion of dairy cows and herds that had a greater proportion of animals registered with a breed society; a reduction in the proportion of cows that calved within the first 42 d of the calving season as well as the proportion of AI used were both associated with a longer mean BLUE for calving interval (Figure 2.5).

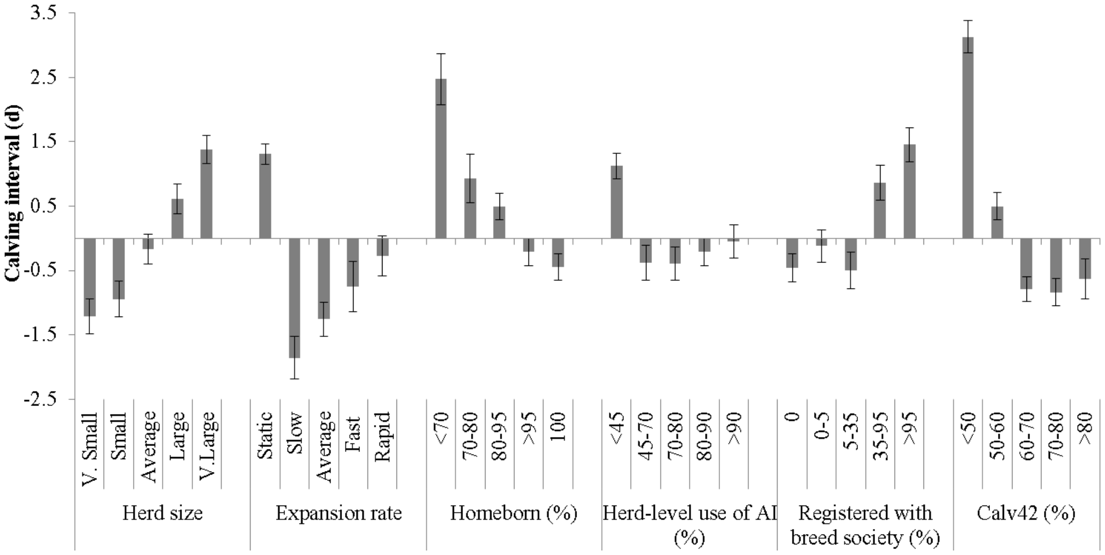


Figure 2.5: Mean (one standard error each side represented as error bars) best linear unbiased estimate for calving interval for each category of six herd-level characteristics.

Inferior mean BLUE for survival was associated with an increase in herd size, a static expansion rate and an increase in the number of animals purchased in. An increase in the proportion of animals registered with a breed society and a decrease in the proportion of AI used were both associated with poorer mean BLUE for survival. The proportion of cows that calved within the first 42 d of the calving season had no obvious association with mean BLUE for survival (Figure 2.6).

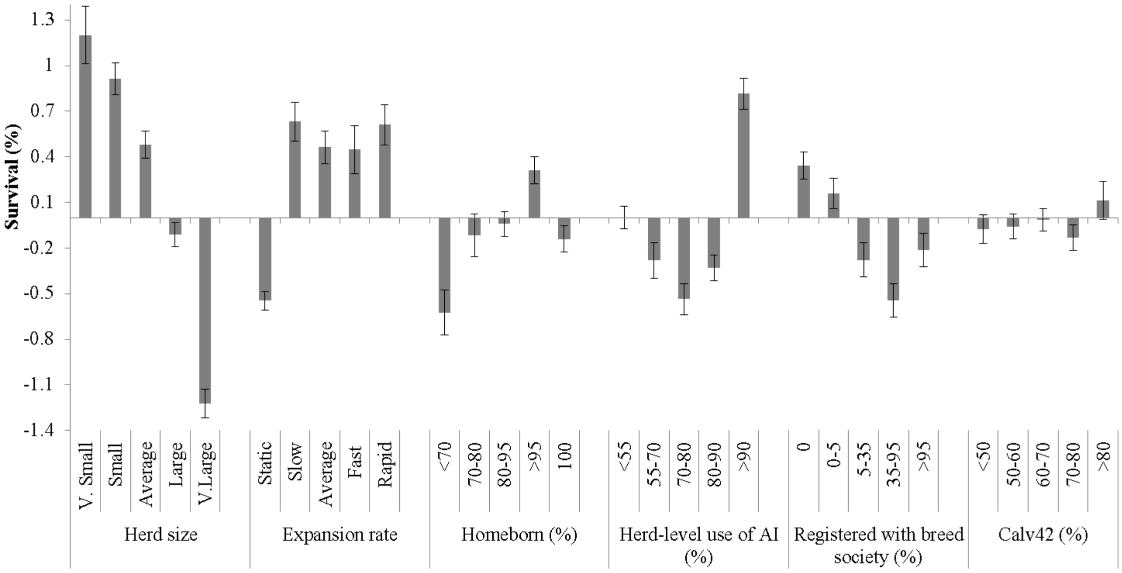


Figure 2.6: Mean (one standard error each side represented as error bars) best linear unbiased estimate for survival for each category of six herd-level characteristics.

There was a tendency for mean BLUE for milk yield to increase in association with both a reduction in herd size and a slower rate of expansion; an increase in mean BLUE for milk yield was associated with a greater proportion of cows born on-farm, a greater proportion of AI used, as well as a greater proportion of cows that calved within the first 42 days of the calving season. A large increase in mean BLUE for milk yield was associated with an increased proportion of animals registered with a breed society (Figure 2.7).

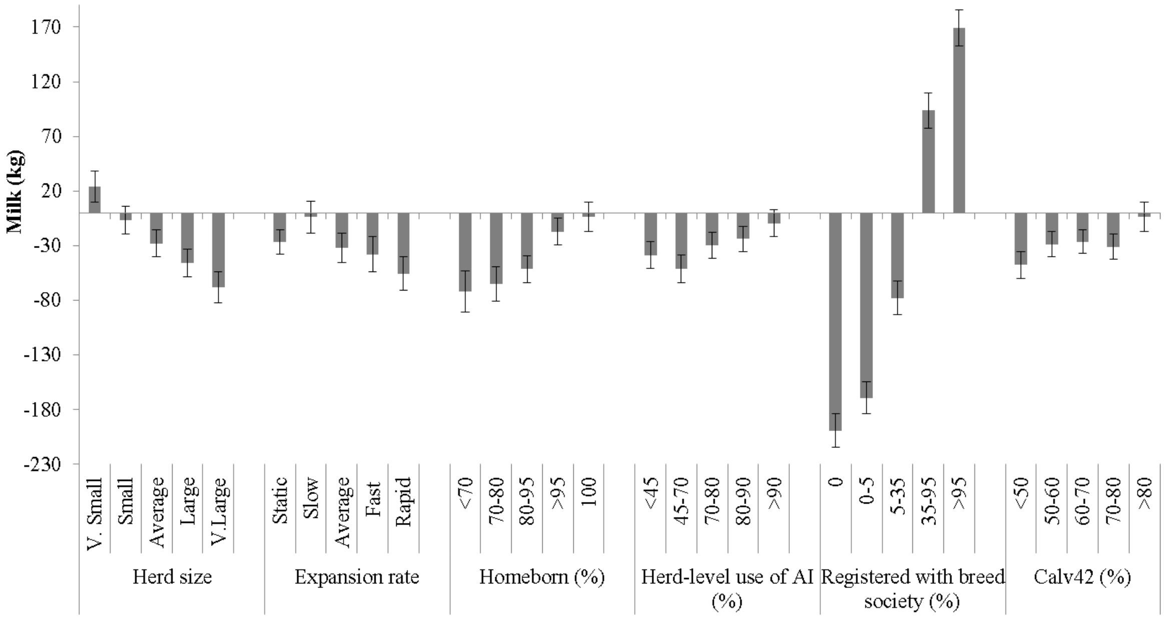


Figure 2.7: Mean (one standard error each side represented as error bars) best linear unbiased estimate for milk yield for each category of six herd-level characteristics.

2.5 Discussion

The motivation for the present study was to quantify the inter-herd variability in performance in a given year after accounting for differences in genetic merit but also elucidate the factors associated with the herd-year phenotypic performance independent of genetic merit. The overall goal was to establish the usefulness of BLUEs in herd management decision support tools and what factors would need to be considered when attempting to explain differences in herd solutions to producers. For example, what was quite clear from the present study was that the mean herd performance for a range of traits differed substantially across geographical locations which could, of course, be attributable to a multitude of factors, not least the climatic conditions pertinent to each geographical location. Hence, when benchmarking herds on performance, firstly differences in the mean genetic merit of the herd should be accounted for, and then consideration should be taken of geographical location as well as the other factors reported in the present study to be associated with herd-year BLUE solutions. Moreover, the expected impact on performance of a herd transitioning between different states of the herd-level factors (e.g., a rapidly expanding herd slowing down to eventually become a static herd) can be predicted and relayed to the producer as well as being used to explain why a herd’s performance may differ from expectation.

2.5.1 Mean annual best linear unbiased estimates versus best linear unbiased predictors

Although the annual least square means herd-year BLUE for calving interval tended to fluctuate by year, a linear regression line fitted through all 9 years’ BLUEs revealed a mean annual reduction of 1 d (SE = 0.30, $R^2 = 0.63$). The linear regression coefficient fitted through all years’ BLUPs for calving interval was -0.33 (SE = 0.01, $R^2 = 0.99$), whilst the regression coefficient fitted to the raw annual calving interval values was -1.54 (SE = 0.29, $R^2 = 0.81$). This indicates that the observed additive genetic improvement contributed to 21.75% of the improvement in the raw phenotype for calving interval, with BLUEs contributing to a further 67.89%. Similarly, the annual least square means herd-year BLUE for milk yield also fluctuated by year; after a linear regression was fitted through the 10 years’ data for milk yield, it revealed that from the sum of the BLUE and BLUP regression coefficients, BLUEs contributed to 69% (regression coefficient = 17.69, SE = 17.99, $R^2 = 0.11$) of the improvement in milk yield. Although it has previously been suggested, that between the years 1980 and 2004, additive genetic merit was the main contributor (63%) to the deterioration in calving interval of Irish dairy cow (Berry et al., 2014), the present study suggested the change in genetic merit is only contributing 21.75% to the improvement. Whilst the current relative contribution of additive genetic merit to the raw phenotype may be considered low in comparison to previously described, breeding programs still offer an opportunity for cumulative and permanent gains to be achieved with the performance of the current generation being a function of the genetic improvement in previous generations. Moreover, it should be noted that the approximate replacement rate on dairy farms is 20%; therefore only 20% of the herd being replaced annually will benefit from the change in genetic merit.

The repeatability of herd-year BLUEs may be of particular interest for, not only the individual producer, but the dairy processors, and the wider dairy sector as a whole, owing to the predictability of the herd performance. The high repeatability of herd-year BLUE for milk yield implies that the herd performance of future years can be predicted with reasonable accuracy despite the likely contributions of external factors such as weather conditions, milk price volatility and feed input costs. In the present study, 74% of the top 20% yielding dairy herds are predicted to remain in this category in the subsequent year (Table 2.3). The benefit of forecasting production would be to enable milk processors predict the quantities of milk in the following production year, leading to more secure production contracts and manufacturing planning. The fact that the fertility traits in the present study (i.e., calving interval, calving to first service interval and number of services) were lowly repeatable over years implies that extension service providers must continually emphasize the importance of consistently achieving key performance indicators as well-performing herds in any year may not necessarily perform well in subsequent years.

2.5.2 Tailored decision support

Extension services and the associated advice provided to producers on how to achieve key performance indicators have traditionally been relatively generic. In general, such advice has been to use the best germplasm available and adopt the associated best management practices. Anecdotally, in fact, poor breeding choices are often blamed for poor phenotypic herd performance, despite the choice of herd management practices in place on farm having a critical role in the realisation of the genetic potential of the animals. There is clearly a gap in the market for tailored decision support tools to more distinctly differentiate between the contributing factors to the observed performance and thus where the resources should be exerted to achieve gains in performance. Bastin et al. (2009) recognised this necessity and proposed that milk urea concentrations in dairy cow milk could potentially be used as a tool to provide producers with feed management decision support owing to the relationship between milk urea and protein metabolism. Similarly Caccamo et al. (2008) proposed that by identifying sources of herd-level variation in milk components and somatic cell count, management decision support tools could be developed that would quantify how different levels of management contribute to the identified sources of variation. In fact, the benefit of using BLUEs to disentangle the contribution of both genetic merit and management to the observed performance has the potential to be applicable to a whole range of different performance characteristics and species; Englishby et al. (2017), for example, proposed using BLUEs from random regression models on carcass weight as a tool to quantify herd-level effects on carcass growth rates and other beef carcass trait profiles.

The usefulness and applicability of BLUEs in the context of the data explored in the present study is illustrated, by means of an example, in Figure 2.8 for calving interval, just for the 2015 calendar year. Despite the herd-year raw mean phenotypic calving interval for two herds only differing by 0.42 d (i.e., herds 1 and 6 in Figure 2.8), clear differences in the BLUEs for these herds existed after adjusting for the fixed and random effects in the genetic evaluation model; the fixed effects in the national genetic evaluations are age at calving, heterosis and recombination loss. Based on the herds in Figure 2.8, the BLUE calving interval for herd 1 lengthened, whilst the BLUE calving interval for herd 6 shortened; the mean calving interval EBV of the cows in herds 1 and 6 in the year 2015, was -5.57 d (very good) and 0.00 d (average), respectively. Therefore, the producers in herd 6 should focus more on breeding for superior fertility whilst herd 1 may consider focusing on improving management to reap the benefit of its superior genetic merit; in this case, the farm advisor could attribute the suboptimal performance to some of the factors identified in the present study, for instance, expansion rate as well as other herd-level factors, such as level of heat detection monitoring. Using another example of two herds from Figure 8, herd 5 had the longest raw mean phenotypic calving interval (13.23 d) whilst herd 3 had the shortest raw mean phenotypic calving interval (-

4.42 d); the respective BLUEs for these herds ranked opposite (+0.80 d and +7.39 d, respectively) after adjusting for the genetic merit of the herds (and other fixed effects in the genetic evaluation model).

When analysing a sample set of herds in the year 2015 for milk yield, a similar phenomenon also existed when comparing raw herd means for milk yield and the respective BLUEs (Figure 2.9). Unlike calving interval, the difference between the individual raw phenotypic performance and the corresponding herd BLUE was predominantly explained by the herds' EBV; this suggests that, depending on the trait, and therefore its heritability, the contribution of differences in EBVs to the disparity between raw and BLUEs differs. If the trait was highly heritable (e.g., milk yield), the herd's mean EBV explained the majority of the difference between the raw and BLUE; however, if the trait was lowly heritable (e.g., fertility (Berry et al., 2013), the difference between the raw and BLUE is only partially explained by herd mean EBV.

Two herd-level factors that were noticeably associated with herd BLUEs for all traits investigated in the present study were expansion rate and herd size, both of which have also been previously reported to be associated with various performance traits in spring-calving dairy cow herds (Jago and Berry, 2011). Jago and Berry (2011) stated that faster expanding herds had a shorter raw calving interval than static herds, and these findings were similar to the present study which stated that slow, average and fast rates of expansion were associated with shorter caving intervals in comparison to static herds. However, in direct contrast to Jago and Berry (2011), smaller herd sizes in the present study had, on average, shorter calving intervals.

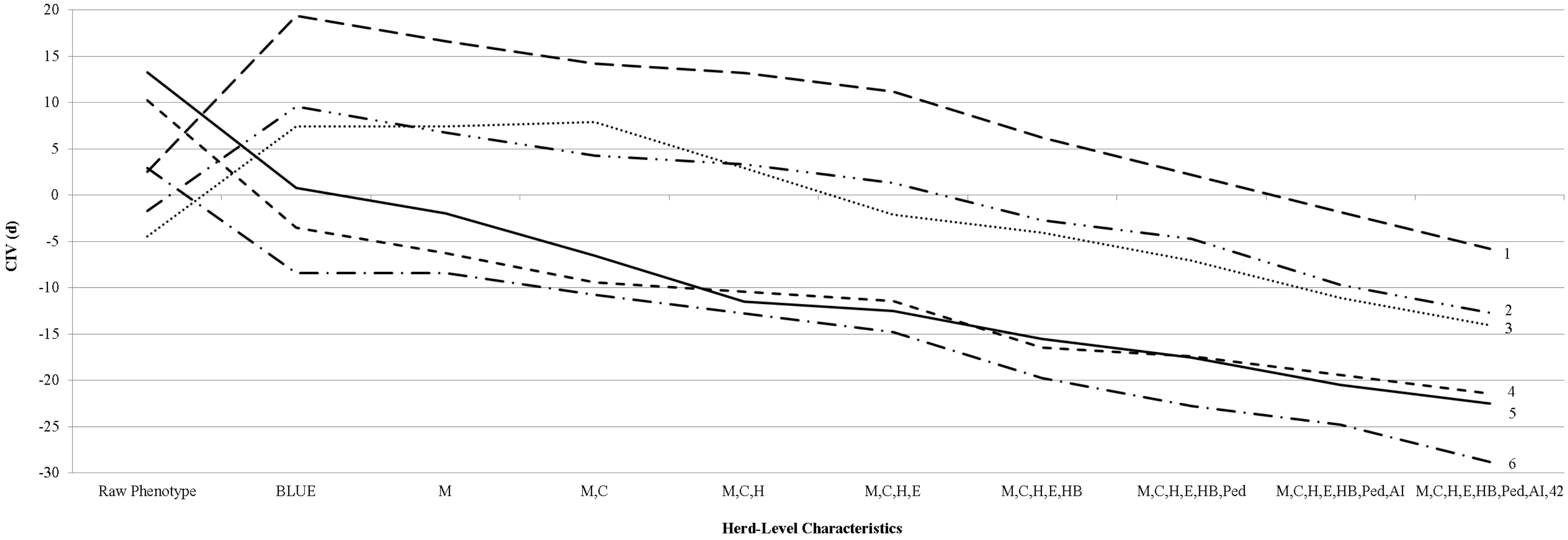


Figure 2.8: The cumulative change in raw phenotypic performance of calving interval for six individual herds (1 (— —), 2 (— ··), 3 (···), 4 (---), 5 (——), 6 (— ·)) after adjusting for each herd-level characteristic separately; the initial change from Raw Phenotype to BLUE adjusts for fixed effects, followed by if the herd milk recorded or not (M), the herds geographical location on county level (M,C), the size of herd (M,C,H), the expansion rate of the herd (M,C,H, E), the proportion of animals home-born (M,C,H, E, HB), the proportion of animals registered with breed society (M,C,H, E, HB, Ped), the proportion of AI use on farm (M,C,H, E, HB, Ped, AI) and finally, the proportion of cows that calved within the first 42 days of the calving season (M,C,H, E, HB, Ped, AI, 42).

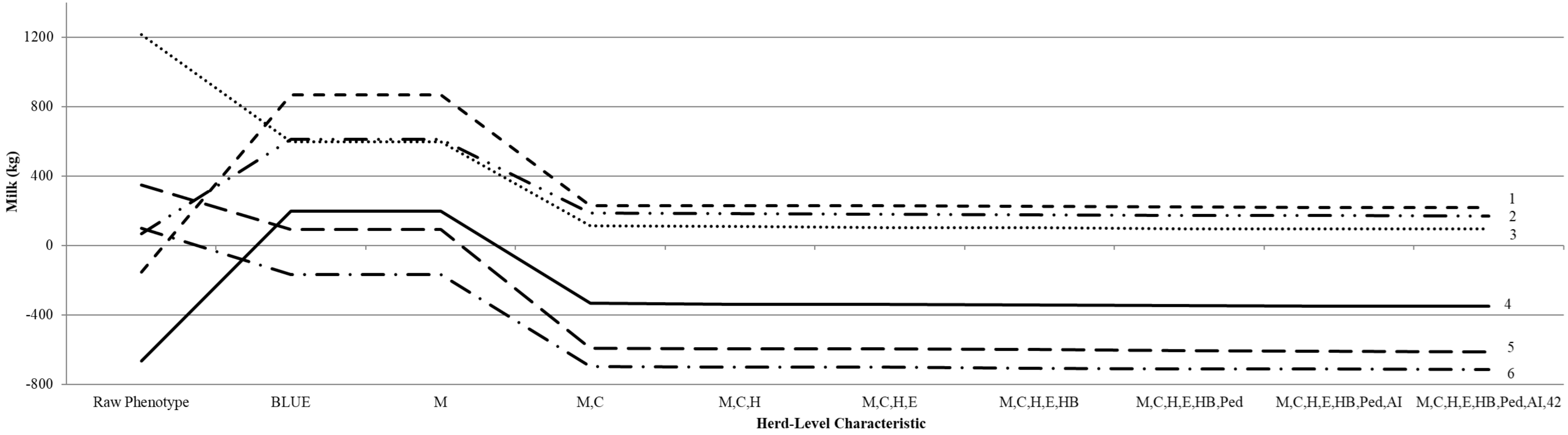


Figure 2.9: Change in raw phenotypic performance of milk yield for six individual herds (1 (----), 2 (— ··), 3 (···),4 (——), 5 (— —), 6 (— ·)) after adjusting for each herd-level characteristic separately; the initial change from Raw Phenotype to BLUE adjusts for fixed effects, followed by if the herd milk recorded or not (M), the herds geographical location on county level (M,C), the size of herd (M,C,H), the expansion rate of the herd (M,C,H, E), the proportion of animals home-born (M,C,H, E, HB), the proportion of animals registered with breed society (M,C,H, E, HB, Ped), the proportion of AI use on farm (M,C,H, E, HB, Ped, AI) and finally, the proportion of cows that calved within the first 42 days of the calving season (M,C,H, E, HB, Ped, AI,42).

The impact of geographical location on the mean BLUEs for milk yield ranged from -365 kg to 1,915 kg; the highest yielding county surrounded the country's capital and the majority of dairy producers in this location produce liquid milk achieved through the feeding of more concentrates; the lowest yielding region was predominantly a mountainous region. The impact of accounting for geographical location when explaining differences in BLUEs was clearly evident when comparing the example herds in Figure 9 for milk yield. Changing farm location is not, of course, possible, but when producers are benchmarking key performance indicators, it is important that they are being compared to contemporaries, which in that case would imply altering the herd BLUEs based on the model solutions for geographical location estimated in the present study. The remaining herd-level characteristics had minimal impact on the BLUE for milk yield.

2.6 Conclusion

Increased efficiency of production and optimising the use of available resources should be based on pertinent advice tailored to each farm with a strategy on where to focus resources to achieve the greatest gains. At a macro-level, animal genetic merit and herd management are the two factors dictating the observed performance and, at the very least, a differentiation should be made between these as to which is the most likely limiting factor. At a management level, some factors (e.g., geographical location) are unavoidable and benchmarking of performance should take this into consideration; similarly, some factors may be transient such as herd expansion rate. BLUEs, and the appropriate analysis of such, can provide useful information to tailor decision support tools for individual herd managers. As BLUEs are already routinely generated from (national) genetic evaluations, no extra resources are required other than to develop the decision support infrastructure. What is not yet known however, is whether the extent of the association between the (estimated) genetic merit for a trait and its respective phenotypic performance differs depending on the herd BLUE; such information would further the precision of breeding specific support tools (i.e. matching the recommended germplasam to herd-specific conditions).

Chapter 3: How herd best linear unbiased estimates affect the progress achievable from gains in additive and non-additive genetic merit

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3.1 Abstract

Sustainable dairy cow performance relies on the coevolution in the development of breeding and management strategies. Tailoring breeding programs to herd performance metrics facilitates improved responses to breeding decisions. While herd-level raw metrics on performance are useful, implicitly included within such statistics is the mean herd genetic merit. The objective of the present study was to quantify the expected response from selection decisions on additive and non-additive merit by herd performance metrics independent of herd mean genetic merit. Performance traits considered in the present study were age at first calving, milk yield, calving to first service, number of services, calving interval and survival. Herd-level best linear unbiased estimates (BLUEs) for each performance trait were available on a maximum of 1,059 herds, stratified as best, average and worst for each performance trait separately. The analyses performed included 1) the estimation of (co)variance for each trait in the three BLUE environments and 2) the regression of cow-level phenotypic performance on either the respective estimated breeding value (EBV) or the heterosis coefficient of the cow. A fundamental assumption of genetic evaluations is that one unit change in EBV equates to a one unit change in the respective phenotype; results from the present study, however, suggest that the realisation of the change in phenotypic performance is largely dependent on the herd BLUE for that trait. Herds achieving more yield, on average, than expected from their mean genetic merit, had a 20% greater response to changes in EBV as well as 43% greater genetic standard deviation relative to herds within the worst BLUE for milk yield. Conversely, phenotypic performance in fertility traits (with the exception of calving to first service) tended to have a greater response to selection as well as a greater additive genetic standard deviation within the respective worst herd BLUE environments; this is suggested to be due to animals performing under more challenging environments leading to larger achievable gains. The attempts to exploit non-additive genetic effects such as heterosis are often the basis of promoting cross-breeding, yet the results from the present study suggest that improvements in phenotypic performance is largely dependent on the environment. The largest gains due to heterotic effects tended to be within the most stressful (i.e., worst) BLUE environment for all traits, thus suggesting the heterosis effects can be beneficial in mitigating against poorer environments.

3.2 Introduction

Genetic effects (i.e., additive and non-additive) and environmental effects (i.e., permanent and temporary) as well as their interaction and, where relevant, their covariance, determine an animal’s phenotypic performance (Visscher et al., 2008). Dairy cow breeding programs have focused almost exclusively on exploiting the additive genetic portion of the phenotype; crossbreeding strategies attempt to also exploit non-additive genetic effects. Dairy cow genetic evaluations calculate the estimated breeding values (EBVs) of traits independent of measurable management effects, through a process called best linear unbiased prediction (BLUP). It is the EBVs, generally within the framework of an overall breeding objective, that are used to rank animals as candidate parents of the next generation. Such ranking on EBV is undertaken irrespective of the environment/management system their progeny are likely to be exposed to. Moreover, the expectation is that a one unit difference in EBV should equate to a one-unit difference in performance (in the average environment). The existence of genotype-by-environment interactions contribute to a deviation from the expectation and such deviations have been documented in dairy cattle (Craig et al., 2018), beef cattle (Ferreira et al., 2015) and sheep (Pollott and Greeff, 2004). Previous studies, however, stratified herds based on performance which implicitly encapsulates the total genetic merit of the contributing animals. In the process of genetic evaluations, both fixed effects solutions (best linear unbiased estimates; BLUE) and random effects solutions (BLUP) are generated, each being independent of the other. Therefore, arguably, a more logical strategy to quantify the extent of genotype-by-environment interactions (G × E) would be to compare the expected response to selection across herds divergent on BLUE. To our knowledge, there is a void in the scientific literature on such an approach. Furthermore, interest in dairying is intensifying in crossbreeding strategies as a means to introduce added benefit from the resulting heterosis; while the presence of heterosis-by-environment interactions have been cited in dairy cows populations (Bryant et al., 2007; Penasa et al., 2010; Kargo et al., 2012), there is a paucity of information on such interactions where the environments investigated are based on herd-level BLUEs. The objective of the present study was firstly to investigate the existence of G × E interactions across fertility, production and survival traits by stratifying herds based on BLUE performance rather than phenotypic performances thus excluding genetic effects. Secondly, the results from the present study aim to estimate the gains achievable when improving animal-level breeding values within three environments stratified on BLUEs. Finally, the third objective of the present study was to identify the type of environment (e.g. superior versus poor) stratified on BLUEs that expressed non-additive genetic effects such as heterosis and estimate gains attainable within each environment from heterotic effects.

3.3 Materials and Methods

Data used in the present study were obtained from the Irish Cattle Breeding Federation national database, Bandon, Co. Cork, Ireland (http://www.icbf.com).

3.3.1 Quantifying Best Linear Unbiased Estimates

The Irish national fertility genetic evaluation for dairy cows is a 23 × 23 multi-trait and multi-breed evaluation operated using the MiX99 software suite (MiX99 Development Team, 2015) in which each parity is treated as a separate trait. Traits evaluated in the multi-trait evaluation include age at first calving (AFC; i.e. the number of days from birth to first calving), milk yield (kg; based on a 305-d lactation yield) for parity 1 to 5 inclusive, calving to first service interval parity 1 to 3 inclusive (CFS; i.e. the number of days from calving to the cow receiving her first service), number of services (NS) parity 1 to 3 inclusive and calving interval from parity 1 to 5 inclusive (CIV; i.e. the number of days between subsequent calving events). Survival is evaluated as a binary trait based on parity 1 to 5 (inclusive) and is recorded as 1 for lactation x-1 where a recorded calving date existed for lactation x, otherwise as 0 (Berry et al., 2013). Fixed effects included in all models are age at calving (unless age at first calving was the dependent variable), heterosis and recombination loss coefficients; heterosis coefficients were split into separate Holstein × Friesian (HO × FR), Holstein × Jersey (HO × JE), Holstein × Montbelliarde (HO × MO), Holstein × Meuse Rhine Yssel (HO × MY), and Shorthorn × Holstein-Friesian (SR × HF) coefficients. Contemporary group of herd-year-season of calving or birth (AFC) is also included as a fixed effect. Within the genetic evaluation, contemporary group (HYS) effects are defined using methodology outlined in Berry et al. (2013) formed based on algorithms proposed by Crump et al. (1997) and Schmitz et al. (1991); animals within the same herd are grouped based on their calving dates or birth dates (in the case of AFC). The fixed effects and random effects solutions of 3,445,158 dairy cows were obtained from the August 2017 national genetic evaluation for use in the present study.

3.3.2 Data editing for herd-level best linear unbiased estimations

Contemporary group BLUEs for the years 2012 to 2014 (inclusive) and individual animal EBVs were extracted from the national genetic evaluation, for actively milk recording, spring-calving herds. Spring-calving herds, predominate in Ireland (Berry et al., 2013), were defined as herds calving at least 80% of their cows between January and June (inclusive). Data from 4,129 herds were available for analysis. Parity-level BLUE solutions for each trait were initially base adjusted to a common base population; the base population comprised of 152 milk recording herds that had a minimum of 3 records for AFC as well as a minimum of 4 records available for parity 1 to 3 inclusive for NS, CFS and parity 1 to 5 for CIV, survival and milk yield between the years 2012 to 2014 inclusive. A single collapsed herd-year BLUE for each trait was calculated as the average of each HYS estimate in the herd, weighted by the number of animal records within each HYS (Chapter 2). Subsequently, the single collapsed herd-year BLUE was calculated to be relative to the mean of the sample population.

Herds were removed from the study if they did not meet the following criteria during the study period: 1) herds were required to have a BLUE available for all 6 investigated traits; 2,185 herds remained, 2) a minimum of 5 records within each contemporary group were required for at least two of three parities for CFS or NS, and four of five parities for CIV, SU and milk yield (Chapter 2); 1,911 herds remained, 3) herds were required to have phenotypic data available on a minimum of 45 animals and 30 calving events per year; where AFC was the trait analysed, herds were required to have at least 10 heifers calving for the first time each year. The final dataset comprised 1,764 herds with 124,352 animals available for AFC analysis and 216,270 animals available for the analysis of the other performance traits.

3.3.3 Stratifying Herd BLUEs for validation population

A single weighted herd BLUE was calculated by averaging the respective herd-year BLUEs across the three years of data. Herds were ranked on each trait separately. After stratifying the herd-BLUEs into five strata, only the first, third and fifth stratum which represented the top, average and bottom performing twenty percentiles, respectively were retained. As herd BLUEs were stratified based on each trait individually, herds could rank differently for each trait. The final data set analysed for AFC, CFS, NS, CIV, survival, and milk yield contained 1,059 herds (71,721 animals), 1,058 herds (125,736 animals), 1,058 herds (130,607 animals), 1,059 herds (125,035 animals), 1,058 herds (125,934 animals) and 1,058 herds (131,695 animals), respectively. The phenotypic records of animals within the retained herds were masked and the genetic evaluation re-run with the remaining 3,234,629 animals; this was done to generate EBVs for animals within the retained herds without their own performance data contributing to their EBVs. The EBVs generated from the subsequent genetic evaluation were then base adjusted to a base population of 414 Holstein-Friesian AI sires that were born between 2000 and 2005, inclusive.

3.3.4 Statistical analyses

Two separate approaches were used to quantify the extent of genotype-by-environment interactions. Firstly (co)variance component analyses were undertaken using a series of within-trait bivariate sire linear mixed models in ASReml (Gilmour et al., 2009) where the phenotypic performance in each herd BLUE stratum was considered a different trait. The linear mixed model applied to each trait was

$$Y_{ijklmnx} = HYS_j + Parity_k + Heterosis_l + Recombination_m + \sum_{n=1}^{2} age^n + s_x + e_{ijklmno}$$

in which $Y_{ijklmnx}$ = the observed phenotypic performance for AFC, CFS, NS, CIV, survival or milk yield of animal *i* in a given BLUE stratum; HYS_j = the fixed effect of contemporary group; $Parity_k$ = the fixed effect of the *k*th parity (i.e., 1, 2, 3, 4, 5) of the animal *i* (not included in AFC); age^n = the covariate of age (linear and quadratic) of animal *i* (not included in AFC); $Heterosis_l$ = the covariate representing the total heterosis coefficient *l* of animal *i; $Recombination_m$* = the covariate representing the recombination coefficient *m* of animal *i*; s_x = the random effect of the sire additive genetic component of animal *i* where $s \sim N(0, \mathbf{A}\sigma^2_s)$ with $\sigma^2{}_s$ representing the additive genetic variance of the sire and **A** the additive genetic relationship matrix among sires; $e_{ijklmnx}$ = random residual effect, where $e \sim N(0, \mathbf{I}\sigma^2_e)$ with σ^2_e representing the residual variance with a separate residual variance fitted for each BLUE stratum; while a separate residual variance was estimated in each environment, no residual covariance was assumed between records in the different environments. Therefore, the detailed (co)variance structure for a two-trait bivariate analysis between trait x and y was:

$$\begin{bmatrix}\boldsymbol{s}_x\\ \boldsymbol{s}_y\end{bmatrix} = N\left(\begin{bmatrix}\boldsymbol{0}\\ \boldsymbol{0}\end{bmatrix}, \begin{bmatrix}\boldsymbol{A}_{xx}\sigma^2_{s_x} & \boldsymbol{A}_{xy}\sigma_{s_{xy}}\\ \boldsymbol{A}_{yx}\sigma_{s_{yx}} & \boldsymbol{A}_{yy}\sigma^2_{s_y}\end{bmatrix}\right)$$

$$\begin{bmatrix}\boldsymbol{e}_x\\ \boldsymbol{e}_y\end{bmatrix} = N\left(\begin{bmatrix}\boldsymbol{0}\\ \boldsymbol{0}\end{bmatrix}, \begin{bmatrix}\boldsymbol{I}\boldsymbol{\sigma}^2_{\boldsymbol{e}_x} & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{I}\boldsymbol{\sigma}^2_{\boldsymbol{e}_y}\end{bmatrix}\right)$$

where $\boldsymbol{A}$ is the numerator relationship matrix; $\sigma^2_{s_x}$, $\sigma^2_{s_y}$ $\sigma_{s_{xy}}$ and $\sigma_{s_{yx}}$ represent the sire genetic (co)variance parameters of the sires in BLUE stratum x and y, respectively and $\sigma^2_{e_x}$ and $\sigma^2_{e_y}$ are the residual variance in BLUE stratum x and y, respectively. The estimated genetic variance in each stratum was obtained as four times the estimated sire variance. Whether the variance components in each herd BLUE stratum differed from each other was determined using a likelihood ratio test of nested models comparing an unconstrained model to a model where the genetic variance in each stratum of the bivariate analysis were constrained to be equal. Heritability estimates were calculated using ASReml (Gilmour et al., 2009) by dividing the genetic variance (i.e., 4 times the sire genetic variance) by the phenotypic variance (i.e., the sum of the residual and genetic variance). In the second analysis strategy, multivariate linear regression models were used to regress each phenotypic performance trait on its respective EBV in each of the three BLUE strata for all performance traits using PROC MIXED in SAS 9.4 software (SAS Institute Inc., Cary, NC). The linear regression model fitted for all traits was:

$$Y_{ijklmnop} = HYS_j + Parity_k + BLUE_l \mid \sum_{m=1}^{6} Heterosis_m + \sum_{n=1}^{2} age^n$$

$$+ BLUE_l \vert\, EBV_o + BLUE_l \vert\, recombintation_p + e_{ijklmnop}$$

where $Y_{ijklmnop}$ = the observed phenotypic performance for AFC, CFS, NS, CIV, survival or milk yield of animal i in BLUE stratum l; HYS_j = the fixed contemporary group effect; $Parity_k$ = the fixed effect of the kth parity (i.e., 1, 2, 3, 4, 5) of animal i (not included when the dependent variable was AFC); $BLUE_l$ = the fixed effects of lth BLUE stratum (n = 3); $Heterosis_m$ = the covariate representing the heterosis coefficient m of animal i for the breed crosses HO × FR, HO × JE, HO × MO, HO × MY, SR × HF and “other”; age^n = the covariate of age (linear and quadratic) of animal

i (not included when the dependent variable was AFC); EBV_o = the estimated breeding value o for animal i; $recombintation_p$ = the covariate representing the total recombination coefficient value p of animal i; $e_{ijklmnop}$ = the residual error effect.

3.4 Results

Mean phenotypic performance for all traits improved as the respective herd mean BLUE stratum improved (Table 3.1). Similarly, the mean EBV for 305-d milk yield improved as herd stratum for mean milk BLUE improved, differing by 163 kg between the best and worst strata. Herds with the shortest EBV for AFC and CIV were within the respective average stratum, the longest (i.e., worst) EBV for AFC was within the best stratum whereas the longest (i.e., worst) EBV for CIV was within the worst stratum (Table 3.1). The mean EBV for CFS was longest (i.e., worst) in the best stratum for CFS, whilst no differences existed between the average and worst strata for CFS ($P = 0.535$). The mean EBV for NS differed ($P < 0.05$) between the three BLUE strata for NS whilst the EBV for survival only differed ($P < 0.001$) between the best and worst herd BLUE strata for survival (Table 3.1).

3.4.1 Genotype-by-environment interactions

The largest genetic standard deviation for AFC was within the worst stratum for AFC, being 2.5 times greater ($P = 0.001$) than the genetic standard deviation of AFC in the average stratum. As the BLUE for milk yield improved, the genetic standard deviation of milk yield increased by a factor of 1.43 ($P < 0.001$) between the worst and best strata for milk yield (Table 3.2). The genetic standard deviation for NS was 3.25 times larger ($P < 0.001$) in the worst NS BLUE stratum than the best stratum for NS BLUEs. No differences existed in the genetic standard deviation of survival between the three BLUE strata for survival (Table 3.2). With the exception of AFC, the genetic correlations between strata for the remaining traits were all ≥0.827, thus indicating that re-ranking effects are absent across the different BLUE strata (Table 3.2). Genetic correlations for AFC ranged from -0.504 (between the best and worst stratum) to 0.514 (between the average and worst stratum) (Table 3.2). There was a tendency for the largest residual standard deviation to be within the worst BLUE environment and smallest residual variance to be within the best environment for all traits with the exception of milk yield and CFS (Table 3.3). The heritability of milk yield increased as the herd environment BLUE improved ranging from 33% to 50% (Table 3.3). With the exception of CIV, the heritability estimates for the remaining fertility traits tended to increase as the respective environment worsened, ranging from 0.01 to 0.02 (Table 3.3).

Table 3.1: Mean (standard deviation in parenthesis) phenotypic performance, herd best linear unbiased estimate (BLUE) and estimated breeding value (EBV) of animals within herds stratified as best, average and worst for the BLUE of the respective performance trait.

		Herd Rank		
Trait	Mean	Best	Average	Worst
Age at first calving (d)	Phenotype	727.10 (34.51)^{a}	743.59 (55.30)^{b}	809.63 (133.29)^{c}
	BLUE	-35.16 (7.17)^{a}	-18.70 (11.87)^{b}	47.23 (66.80)^{c}
	EBV	10.31 (4.86)^{a}	9.86 (4.81)^{b}	10.04 (5.14)^{c}
Milk yield (kg)	Phenotype	7130.95 (1254.17)^{a}	6060.68 (1077.15)^{b}	4941.22 (1081.84)^{c}
	BLUE	1004.88 (515.95)^{a}	-10.94 (224.23)^{b}	-1043.69 (429.05)^{c}
	EBV	-451.33 (292.13)^{a}	-511.94 (280.94)^{b}	-614.27 (304.03)^{c}
Number of services (u)	Phenotype	1.132 (0.37)^{a}	1.434 (0.68)^{b}	1.744 (0.98)^{c}
	BLUE	-0.302 (0.10)^{a}	-0.013 (0.10)^{b}	0.298 (0.20)^{c}
	EBV	-0.049 (0.06)^{a}	-0.050 (0.06)^{b}	-0.047 (0.06)^{c}
Calving to first service (d)	Phenotype	67.789 (23.16)^{a}	76.294 (21.91)^{b}	84.299 (23.67)^{c}
	BLUE	-8.739 (5.77)^{a}	0.325 (4.10)^{b}	8.730 (6.64)^{c}
	EBV	-2.642 (1.89)^{a}	-2.800 (1.80)^{b}	-2.796 (1.82)^{b}
Calving interval (d)	Phenotype	368.24 (34.35)^{a}	376.43 (48.10)^{b}	395.85 (83.12)^{c}
	BLUE	-11.69 (5.49)^{a}	-2.09 (6.65)^{b}	17.45 (15.93)^{c}
	EBV	-7.02 (4.37)^{a}	-7.41 (4.46)^{b}	-6.25 (4.60)^{c}
Survival	Phenotype	0.918 (0.27)^{a}	0.865 (0.34)^{b}	0.794 (0.40)^{c}
	BLUE	0.060 (0.03)^{a}	0.000 (0.03)^{b}	-0.072 (0.05)^{c}
	EBV	0.007 (0.02)^{a}	0.007 (0.02)^{ab}	0.009 (0.02)^{b}

Different superscripts within a row where $P < 0.05$

Table 3.2: Additive genetic standard deviation for each performance trait within herds stratified as best (top 20%), average (middle 20%) and worst (bottom 20%) based on the best linear unbiased estimates for the respective performance trait as well as the genetic correlations (standard error in parenthesis) between the strata.

	Genetic standard deviation			Correlation		
BLUE Trait	Best	Average	Worst	Best – Average	Best – Worst	Average – Worst
Age at First Calving	14.05^{ab}	12.64^{a}	31.67^{b}	0.275 (0.163)	-0.504 (0.132)	0.514 (0.167)
Milk yield	607.65^{a}	519.96^{b}	423.84^{c}	0.953 (0.014)	0.881 (0.024)	0.936 (0.016)
Calving to First Service	2.39	2.23	2.83	0.869 (0.465)	0.983 (0.142)	0.827 (0.161)
Number of Services	0.04^{a}	0.09^{a}	0.13^{b}	0.912 (0.226)	0.960 (0.216)	0.898 (0.137)
Calving Interval	3.07	5.08	6.81	0.932 (0.276)	0.961 (0.206)	0.905 (0.291)
Survival	0.03	0.04	0.05	0.982 (0.154)	0.882 (0.167)	0.887 (0.151)

Using the chi-square test with 1 degree of freedom to compare likelihood ratio test, different superscripts indicate significance at $P < 0.05$.

Table 3.3: Residual standard deviation for each performance trait within herds stratified as best (top 20%), average (middle 20%) and worst (bottom 20%) based on the best linear unbiased estimates for the respective performance trait as well as the heritability estimates of each trait within the best, average and worst strata.

	Residual standard deviation			Heritability		
BLUE Trait	Best	Average	Worst	Best	Average	Worst
Age at first calving	31.59^a	52.63^b	111.71^c	0.189 (0.028)	0.057 (0.014)	0.079 (0.018)
Milk yield	802.85^a	729.98^b	710.48^c	0.501 (0.029)	0.450 (0.027)	0.327 (0.021)
Calving to first service	18.18^a	17.28^b	19.44^c	0.017 (0.006)	0.017 (0.005)	0.021 (0.006)
Number of services	0.36^a	0.68^b	0.95^c	0.010 (0.005)	0.016 (0.005)	0.018 (0.005)
Calving interval	32.59^a	46.66^b	80.49^c	0.009 (0.005)	0.012 (0.004)	0.007 (0.003)
Survival	0.26^a	0.33^b	0.39^c	0.011 (0.004)	0.013 (0.004)	0.018 (0.004)

Using the chi-square test with 1 degree of freedom to compare likelihood ratio test, different superscripts indicate significance at $P < 0.05$.

3.4.2 Estimated Breeding Value Regression Analyses

The regression of phenotypic survival on the EBV for survival did not differ by herd BLUE strata for either milk yield, CIV or CFS (Table 3.4). Similarly, the relationship between CFS phenotype and the EBV for CFS did not differ by BLUE strata for either CFS or survival (Table 3.4). The regression coefficient of phenotypic AFC on the EBV for AFC within the worst BLUE stratum for AFC was 4 times that in the best BLUE stratum for AFC.

The response in phenotypic milk yield per kg increase in milk EBV in the best milk BLUE stratum was 20% greater than observed in the worst milk BLUE stratum ($P < 0.001$). The regression of phenotypic CIV on the EBV for CIV in the best milk yield BLUE stratum was 1.63 times ($P < 0.001$) that of the regression coefficient in the worst milk BLUE stratum; the corresponding factor for NS was 2.52 ($P < 0.001$). The improvement in phenotypic CFS regressed on the EBV for CFS within the worst milk yield BLUE stratum was 1.67 ($P < 0.01$) times than in the average stratum for milk yield (Table 3.4).

As the BLUE for CIV worsened, the regression coefficient of phenotypic CIV on the EBV for CIV became greater, differing by a factor of 1.62 (between the best and average strata; $P < 0.05$) to 2.63 (between the average and worst strata; $P < 0.001$) compared to the more superior BLUE (Table 3.4). Phenotypic milk yield, CFS and NS regressed on the respective EBV ranged between 1.27 (milk yield; $P < 0.001$) to 1.92 (NS; $P < 0.001$) times greater within the worst stratum BLUE for CIV than the best BLUE stratum for CIV (Table 3.4).

Although no differences existed between the regression coefficients of phenotypic CFS on the EBV for CFS within the three BLUE strata for CFS, the regression coefficient of milk yield on the EBV for milk yield was 1.10 times greater ($P < 0.001$) within the best BLUE stratum for CFS compared to the average BLUE stratum for CFS (Table 3.4). Within the best stratum for CFS, the regression coefficients of CIV and NS on the respective EBVs were 1.28 (CIV; $P = 0.002$) and 1.78 (NS; $P = 0.001$) times greater than that of the respective regression coefficients within the worst BLUE stratum for CFS (Table 3.4).

Phenotypic NS regressed on the EBV for NS was 3.52 times greater (P < 0.001) within the worst BLUE stratum for NS relative to the best stratum for NS, whereas the regression coefficient of phenotypic milk yield and CIV regressed on the respective EBVs was 1.21 (P < 0.001) and 2.66 (P < 0.001) times greater within the worst BLUE stratum for NS than the average stratum for NS (Table 3.4). Within the best stratum for NS, the regression coefficient of CFS on the EBV for CFS was 1.91 (P < 0.001) times greater than in the average stratum for NS. Conversely, within the average stratum for NS, the regression coefficient of survival on the EBV for survival was 1.29 (P = 0.01) times greater than that best BLUE stratum for NS (Table 3.4).

The response in phenotypic survival per unit increase in the EBV for survival was 1.30 times (P = 0.006) greater within the worst stratum for survival relative to the best BLUE stratum. Within the average stratum for survival, the regression coefficients of phenotypic milk yield and NS were 1.13 (P < 0.001) and 1.62 (P = 0.004) times greater, respectively, than in the best stratum for survival. Although the regression coefficient of CIV regressed on the EBV for CIV was 1.57 times greater (P < 0.001) within the average stratum for survival in comparison to the worst stratum, no differences existed between the best and average stratum for survival (Table 3.4).

Table 3.4: Regression coefficients (standard errors within parenthesis) of phenotypic values of each trait regressed on estimated breeding values for each respective trait across the best (top 20 %), average (middle 20 %) and worst (bottom 20 %) strata of best linear unbiased estimates.

		Herd Rank			
BLUEs trait	Trait phenotype	Best	Average	Worst	P- value
Age at first calving (d)	Age at first calving (d)	0.22 (0.12)^{a}	0.46 (0.11)^{a}	0.88 (0.11)^{b}	***
Milk yield (kg)	Milk production (kg)	1.16 (0.01)^{a}	1.01 (0.01)^{b}	0.97 (0.01)^{c}	***
	Calving interval (d)	1.24 (0.06)^{a}	0.82 (0.06)^{b}	0.76 (0.06)^{b}	***
	Calving to first service (d)	0.45 (0.06)^{ab}	0.36 (0.06)^{a}	0.61 (0.06)^{b}	*
	Number of services (unit)	0.83 (0.06)^{a}	0.64 (0.07)^{b}	0.33 (0.06)^{c}	***
	Survival	1.15 (0.07)	0.99 (0.07)	1.10 (0.07)	
Calving to first service (d)	Calving to first service (d)	0.64 (0.07)	0.53 (0.06)	0.59 (0.06)	
	Milk production (kg)	1.28 (0.02)^{a}	1.16 (0.02)^{b}	1.24 (0.02)^{a}	***
	Calving interval (d)	1.20 (0.06)^{a}	0.78 (0.06)^{b}	0.93 (0.06)^{b}	***
	Number of services (u)	0.73 (0.07)^{a}	0.47 (0.06)^{b}	0.41 (0.06)^{b}	**
	Survival	1.05 (0.07)	1.10 (0.07)	1.17 (0.07)	
Number of services (u)	Number of services (u)	0.27 (0.08)^{a}	0.49 (0.06)^{b}	0.95 (0.06)^{c}	***
	Milk production (kg)	1.15 (0.02)^{a}	1.11 (0.02)^{a}	1.34 (0.01)^{b}	***
	Calving interval (d)	0.79 (0.06)^{a}	0.48 (0.06)^{b}	1.28 (0.06)^{c}	***
	Calving to first service (d)	0.69 (0.08)^{a}	0.36 (0.06)^{b}	0.59 (0.05)^{a}	**
	Survival	0.89 (0.07)^{a}	1.14 (0.07)^{b}	1.11 (0.06)^{b}	*
Calving interval (d)	Calving interval (d)	0.35 (0.07)^{a}	0.57 (0.06)^{b}	1.50 (0.06)^{c}	***
	Milk production (kg)	1.19 (0.02)^{a}	1.24 (0.02)^{a}	1.51 (0.02)^{b}	***
	Calving to first service (d)	0.38 (0.07)^{a}	0.35 (0.06)^{a}	0.65 (0.06)^{b}	**
	Number of services (u)	0.42 (0.08)^{a}	0.60 (0.06)^{a}	0.81 (0.08)^{b}	**
	Survival	1.07 (0.08)	1.07 (0.07)	0.92 (0.07)	
Survival	Survival	0.94 (0.08)^{a}	1.07 (0.06)^{ab}	1.22 (0.07)^{b}	*
	Milk production (kg)	1.20 (0.02)^{a}	1.36 (0.01)^{b}	1.24 (0.01)^{a}	**
	Calving interval (d)	1.02 (0.07)^{a}	1.12 (0.05)^{a}	0.71 (0.06)^{b}	***
	Calving to first service (d)	0.57 (0.08)	0.42 (0.06)	0.52 (0.06)	
	Number of services (u)	0.46 (0.08)^{a}	0.74 (0.06)^{b}	0.59 (0.06)^{ab}	*

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Different superscripts within a row where $P < 0.05$

3.4.3 Heterosis Coefficient Regression Analysis within BLUE stratum

The regression of phenotypic AFC on the HO × JE heterosis coefficient was 3.65 times greater ($P = 0.04$) within the worst BLUE stratum for AFC than within the best BLUE stratum for AFC (Table 3.5). Phenotypic milk yield regressed on the HO × JE heterosis coefficient was greatest in the average milk BLUE stratum, being 4.37 times greater than in the best milk BLUE stratum ($P < 0.001$) and 1.40 times greater ($P < 0.05$) than in the worst milk BLUE stratum. The regression coefficient of phenotypic milk yield on the HO × FR heterosis coefficient was 1.86 times greater ($P < 0.001$) in the worst milk BLUE stratum relative to the best stratum (Table 3.5). The regression of phenotypic CFS, NS and CIV on the HO × JE heterosis coefficient was 1.86 (CIV) to 2.24 (NS) times greater within the respective worst BLUE stratum than the best BLUE stratum. Within the worst BLUE stratum for CIV, the regression coefficient of phenotypic CIV on the HO × FR heterosis coefficient was almost 12 times ($P < 0.001$) that in the best BLUE stratum for CIV. Phenotypic survival regressed on the HO × FR heterosis coefficient was 3.33 times greater ($P < 0.001$) within the worst stratum for survival in comparison to the best BLUE stratum (Table 3.5). The regression coefficients of phenotypic performance on each of the heterosis coefficients stemming from the breed combinations HO × MO, HO × MY and SR × HF are in Supplementary Table S9.2; while a similar trend existed for all traits (with the exception of CIV), the associated standard errors were large owing to the small representation of these breed crosses in the dataset.

Table 3.5: Linear regression coefficients of phenotypic performance for each trait on Holstein × Friesian heterosis coefficient (HO × FR), Holstein × Jersey heterosis coefficient (HO × JE) and recombination coefficient within each herd best linear unbiased estimate stratum including the significance of the interaction.

	Herd rank			
BLUEs trait	Best	Average	Worst	P-value
Age at first calving (d)				
HO × FR	-3.08 (2.88)	-2.70 (2.65)	4.54 (2.74)	
HO × JE	-3.98 (2.58)^{a}	-7.12 (3.13)^{ab}	-14.53 (4.34)^{b}	*
Recombination	-10.70 (3.66)^{a}	-11.93 (3.6)^{a}	-47.83 (4.28)^{b}	***
Milk yield (kg)				
HO × FR	180.34 (15.96)^{a}	224.09 (16.08)^{a}	336.06 (16.12)^{b}	***
HO × JE	48.62 (30.34)^{a}	212.60 (21.87)^{b}	151.36 (14.89)^{c}	*
Recombination	-357.52 (30.34)^{a}	-78.35 (28.15)^{b}	-127.3 (22.94)^{b}	***
Survival				
HO × FR	0.01 (0.01)^{a}	0.02 (0.01)^{a}	0.04 (0.01)^{b}	***
HO × JE	0.03 (0.01)	0.04 (0.01)	0.04 (0.01)	
Recombination	-0.043 (0.01)^{a}	0.00 (0.01)^{b}	-0.02 (0.01)^{b}	**
Number of services (units)				
HO × FR	-0.03 (0.02)	-0.04 (0.02)	-0.09 (0.02)	
HO × JE	-0.05 (0.03)^{a}	-0.05 (0.02)^{a}	-0.12 (0.02)^{b}	***
Recombination	0.05 (0.03)^{a}	0.05 (0.03)^{a}	-0.01 (0.03)^{b}	*
Calving to first service interval (d)				
HO × FR	-0.60 (0.56)	-0.31 (0.49)	0.65 (0.52)	
HO × JE	2.75 (0.92)^{a}	0.13 (0.56)^{b}	-2.40 (0.51)^{c}	***
Recombination	-1.88 (1.03)	-2.10 (0.82)	-2.79 (0.77)	
Calving interval (d)				
HO × FR	-0.82 (1.26)^{a}	-2.64 (1.09)^{a}	-9.77 (1.22)^{b}	*
HO × JE	-3.26 (1.91)^{a}	-3.31 (1.41)^{a}	-6.04 (1.42)^{a}	*
Recombination	1.07 (2.30)	-0.47 (1.82)	-6.42 (1.95)	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Different superscripts within a row where $P < 0.05$

3.4.4 Recombination Coefficient Regression Analysis within BLUE stratum

The regression of phenotypic AFC on the recombination coefficient was 4.47 times greater (P < 0.001) in the worst stratum than in the best stratum for AFC (Table 3.5). Phenotypic milk yield regressed on the recombination coefficient was 4.56 times greater (P < 0.001) in the best BLUE stratum for milk yield than the respective average stratum (Table 3.5). The regression of phenotypic NS on the recombination coefficient was 2.2 times greater (P < 0.001) within the best BLUE stratum than the worst BLUE stratum for NS (Table 3.5). Phenotypic survival regressed on the recombination coefficient ranged from 0.00 (in the average stratum) to -0.043 (in the best stratum) (Table 3.5).

3.5 Discussion

Breeding programs tailored to the requirements of individual dairy producers are increasingly sought after. The expected performance of the progeny from a given mating is traditionally predicted from the EBV of the progeny converted to a deviation from the mean phenotypic performance of the base animal; such an approach assumes that a one unit difference in EBV equates to a one unit phenotypic difference for that trait. Similarly, if the progeny is crossbred, then a predetermined heterosis effect is added to the respective predicted phenotypic performance to generate an estimate of expected performance (Kelleher et al., 2016). Results from the present study reveal that such simple mathematics are not always valid and, not only does the association between EBV and phenotype differ by environment, but also the association between the heterosis coefficient and phenotype differ by environment; the former phenomenon, commonly known as G × E has been well publicised (Fikse et al., 2003; Haile-Mariam et al., 2008; Craig et al., 2018) while the latter, known as heterosis-by-environment (H × E) interaction, is less well documented in dairy cows (Penasa et al., 2010; Kargo et al., 2012). To our knowledge no study has attempted to quantify the extent of either G × E or H × E where the environment (i.e., E) was represented by a BLUE from a genetic evaluation.

Using a subset of the data used in the present study, in Chapter 2 it was proposed that herd-level BLUEs could be used to categorise dairy herds based on performance independent of genetic effects and systematic environmental effects. The motivation for using the BLUEs was to provide informed decision support systems especially for the identification of herds performing below their genetic potential and, by using the fixed effects solutions from the underlying statistical model, attempt to explain some of the apparent inconsistencies (Chapter 2). Once diagnosed, the next step in a decision support system is to provide solutions to help improve herd performance. While management strategies such as improved animal nutrition, vaccination, or greater attention to reproductive performance could help bridge some of the gap in the difference between expectation and realisation, breeding strategies could also form part of the solution. Results from the present study clearly showed that the realisation of breeding decisions is associated with the environment the animal is/was exposed to, and therefore incorporating such information in a mating advice tool may be beneficial in the prediction of realistic offspring performance. Being able to derive expected performance of offspring for alternative scenarios may also be useful in the evaluation of alternative breeding strategies such as, for example, evaluating the benefit of a cross breeding program.

3.5.1 Genetic variability differs by environment

The observation of a larger genetic standard deviation for milk yield in the high milk BLUE environment (1.43 times than that of the worst milk BLUE; Table 3.2) was consistent with the greater regression coefficient of phenotypic milk yield on the milk yield EBV (1.2 times greater) in the high BLUE than the worst milk BLUE (Table 3.4); this indicates that the mean response to selection for milk yield is greater in the best BLUE for milk yield. The converse was true, however, for the remaining traits representing fertility (with the exception of CFS), AFC and survival, in that the regression coefficient of the phenotypic performance on the respective EBVs ranged from 1.30 (survival) to 4.28 (CIV; d) times larger in the respective worst BLUE environment relative to the best BLUE environment. Similarly, the genetic standard deviation of each trait (except milk yield) was 1.18 (CFS; d) to 3.63 (NS; serves) times larger in the respective worst BLUE environment relative to the respective best BLUE environment. Craig et al. (2018) reported a similar range (1.2 to 3.6 times greater) when estimating the genetic standard deviations of fertility traits (i.e., calving rate within the first 42d of the calving season, calving season day and the percentage mated in the first 21d of the calving season) within low-fertility herd environments relative to high-fertility environments. Low genetic standard deviations for survival within the best respective stratum relative to the worst stratum may be an indication of more stringent voluntary culling decisions, and may explain why the mean EBV for survival was greatest in the worst stratum for survival.

The differential in genetic standard deviations and the regression coefficients of the phenotypic performance on the respective EBV by environment is not novel and has been reported elsewhere in dairy cattle (Craig et al., 2018), beef cattle (Ferreira et al., 2015) and sheep (Pollott and Greeff, 2004). The novelty here, however, was that no study to date has stratified environments based on BLUEs and therefore there was an implicit link between the herd stratum for the performance trait and genetic merit since the mean genetic merit of the herds would have contributed to their eventual phenotypic performance; this is especially true for highly heritable traits such as milk yield. In Chapter 2 BLUEs were analysed in the form of HYS effects and it was reported that from the sum of the regression coefficient of BLUEs and BLUPs fitted through 10 years of data, 69% of the improvement in phenotypic milk yield was as a result of BLUE effects. The greater genetic standard deviation of milk yield in the best BLUE milk yield environment therefore clearly suggests that it is largely a function of the superior management employed in these environments, which in Ireland, could include superior grassland management but also could be due to increased concentrate input. From a controlled experimental study on grazing dairy cows, Coleman et al. (2010) documented a greater response in milk solids to feed intake in higher genetic merit animals (based on a total merit index) from either a greater inclusion of concentrate or grass allowance in the diet.

Greater regression coefficients of fertility phenotypic performances on the respective EBV within the respective worst BLUE stratum are indicative of a greater response to selection for fertility traits in such environments. Yet, unlike milk yield, where poor response to selection is reflective of sub-optimum management, the poor response to selection within the best BLUE fertility trait stratum is reflective of superior management under optimal environmental conditions leading to animals approaching their biological limit or the limit of the production system (i.e., calving intervals of less than 365 are generally not sought at a herd level). Management practice obviously have an impact on reproductive performance as evidenced by a mean phenotypic difference of 27.61 d between the best and worse CIV BLUE despite a mean difference of less than 1 d in EBV for CIV (Table 3.1).

With the exception of AFC, genetic correlations for the same trait in different strata were in the range of 0.827 (between average and worst strata for CFS BLUEs; SE = 0.161) to 0.983 (between best and worst strata for CFS BLUEs; SE = 0.142) (Table 3.2). Mulder et al. (2006) suggested that only genetic correlations between environments of < 0.61 justified consideration of a separate breeding program to optimise genetic gain in the different environments. Although the correlations between BLUE strata for AFC were less than 0.61, AFC is a trait that may reflect largely upon the breeding decisions of the manager and not necessarily the animal's genetic capability; the mating of heifers may be suspended in order to have the animals calving at a particular time of the year, especially in seasonal calving programs (Berry et al., 2013).

3.5.2 Benefits of heterosis differ by environment

Heterosis is a non-additive genetic phenomenon whereby the performance of crossbred progeny, on average, surpasses the mid-parent mean (Simm, 1998). Interest in crossbreeding strategies is increasing in dairy cow production systems as a means to rapidly improve performance, especially for traits associated with viability and fertility (McAllister, 2002; Wall et al., 2005; Sørensen et al., 2008). In some populations, however, the additive genetic merit of one dairy breed may actually be substantially inferior to that of the best available dairy breed. A decision is therefore required as to whether the direct progeny performance would be expected to be superior if crossbreeding was embarked upon (taking cognisance of expected heterosis) versus if straight-breeding with the genetically superior breed was undertaken. An estimate of the mean heterosis effect for different breed combination can be derived from published studies (Dezetter et al., 2015; Coffey et al., 2016) or simply as the fixed effects solutions from routine genetic evaluations.

Results from the present study clearly demonstrate that the benefit of heterosis differs by environment which is consistent with reports elsewhere on production traits in dairy cows (Penasa et al., 2010; Kargo et al., 2012); however, there is a lack of heterosis by environment studies for fertility traits. Based on the results from the present study a) genetic evaluations should take cognisance of this heterosis by environment interaction and b) mating-based decision support systems need to apply the correct heterosis effects, based on herd BLUE, when comparing the mating of parents of the same or different breeds.

Animals within the best BLUE herds for production, fertility and survival tended to experience the least benefit from heterosis, suggesting that heterotic effects are expressed more as the environment becomes increasingly stressful. The extent of heterosis expression, however, seems to be dependent on the breed composition of the F_1 crosses when analysing production traits. Based on Friesian crosses, Penasa et al. (2010) reported a similar trend to the present study whereby the greatest heterosis benefit was within the worst environment for milk yield. Nonetheless, the greatest benefit in milk yield from heterosis when Jersey formed a component of the cross in the present study was within the average herd BLUE for milk yield, which is consistent with Bryant et al. (2007) and Kargo et al. (2012). The heterosis coefficients of the fertility and survival traits were consistently larger in the respective worst BLUE strata (i.e., more stressful environment) relative to the best BLUE strata. This suggests that not only can performance (and profit) be increased in herds with poor BLUEs for fertility and survivability with the exploitation of heterosis effects, but such effects may also promote robustness and resilience amongst animals within challenging environments. Within the Irish national economic breeding index, calving interval has a negative economic value of €12.59 per day (ICBF, 2019g). Therefore, the economic benefit of heterosis in an F_1 HO × FR cross is expected, on average, to be €123 in herds within the poorest BLUE for calving interval but only €10.32 in the herds that are best for calving interval.

3.6 Conclusion

Phenotypic performance is inherently influenced by both the environment and genetic effects as well as how both effects interact with each other. Thus, predicting the additive genetic merit of a progeny from a given mating is suggested to be too simplistic and does not take cognisance of the environmental factors that are likely to have influence the realisation of the genetic merit. By stratifying herds on BLUEs for each trait, the phenotypic response to changes in EBVs differed for milk yield, CIV, NS and AFC between at least two of the three environments investigated. Additive genetic variance for milk yield, AFC and NS was greatest within the environment that had the largest scope for improvement, e.g. the best herd BLUE environment for milk yield and the worst herd BLUE environment for AFC and NS. Hence accounting for the heterogeneity of variances in the genetic evaluation process is important. With the exception of the HO × JE heterosis for milk yield, the benefits of non-additive heterotic effects were greatest in the most stressful environment for each respective trait. Ultimately, the results from the present study reiterate that heterosis is an effect that promotes robustness and resilience and is emphasised when conditions deteriorate. Clear benefits from incorporating BLUEs into a breeding-specific decision support tool can facilitate more precise breeding decisions specific to individual herds.

Chapter 4: Formulation of a decision support tool incorporating both genetic and non-genetic effects to rank young growing cattle on expected market value

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4.1 Abstract

While breeding indexes exist globally to identify candidate parents of the next generation, fewer tools exist that provide guidance on the expected monetary value of young animals. The objective of the present study was therefore to develop the framework for a cattle decision-support tool, which incorporates both the genetic and non-genetic information of an animal and, in doing so, better informs the potential market value of an animal, whatever the age. Two novel monetary indexes were constructed and their predictive ability of carcass value was compared to that of the Irish national Terminal breeding index, typical of other terminal indexes used globally. A constructed Harvest index was comprised of three carcass-related traits (i.e., weight, conformation and fat each weighted by their respective economic value) and aimed at purchasers of animals close to harvest; the second index, termed the Calf index, also included docility and feed intake (weighted by their respective economic value), thus targeting purchasers of younger calves for growing (and eventually harvesting). Genetic and non-genetic fixed and random effect model solutions from the Irish national genetic evaluations underpinned all indexes. The two novel indexes were formulated using three alternative estimates of an animal's total merit for comparative purposes: 1) an index based solely on the animal's breed solutions, 2) an index which also included within-breed animal differences and, 3) an index which, as well as considering additive and non-additive genetic effects, also included non-genetic effects (referred to as production values [PV]). As more information (i.e., within breed effects and subsequently non-genetic effects) was included in the total merit estimate, the correlations strengthened between the two proposed indexes and the animal's calculated carcass market value; the correlation coefficients almost doubled in strength when total merit was based on PV-based estimates as compared to the breed solutions alone. Including phenotypic live-weight data, collected during the animal's life, strengthened the predictive ability of the indexes further. Based on the results presented, the proposed indexes may fill the void in decision support when purchasing or selling cattle. In addition, given the dynamic nature of indexes, they have the potential to be updated in real-time as information becomes available.

4.2 Introduction

Individual animal ranking on beef breeding indexes are widely used to support decisions for selecting candidate parents of the next generation (Berry et al., 2019a); in the absence of genotype-by-environment interactions, the progeny of genetically superior animals are, on average, expected to perform better than the progeny of genetically inferior animals if exposed to the same management conditions. Breeding index values are available in some countries for all cattle from birth irrespective of whether they can even become parents (e.g., steers); these index values, if economic-based, still provide an indication of the expected profit of that animal. The applicability of such breeding indices for live animals destined for slaughter are, however, limited in that: 1) they are constructed solely from an animal's additive genetic merit without cognisance of either the non-additive genetic effects (e.g., heterosis), or the non-genetic effects (e.g. dam parity), and 2) the indexes often include traits which become redundant to the expected profit of a growing animal itself once born (e.g. genetic merit for stillbirth).

Both non-additive genetic effects and non-genetic effects are known to impact the performance of growing cattle. Gregory et al. (1978) carried out extensive research into heterosis values in beef cattle and reported that crossbred calves were weaned 7.4 % heavier than purebred calves. Connolly et al. (2016) documented that third parity cows produced progeny carcasses 1.1 kg heavier than progeny from second parity cows; furthermore, progeny from second parity cows had, on average, 2.04 kg heavier carcasses than progeny from primiparous cows. McHugh et al. (2014) reported that up to the point of weaning, males calves grew 0.17 kg per day faster than female calves. Given that such heterosis and environmental effects exist, then these effects should be incorporated into tools to rank animals on expected profit.

The objective of the present study was to formulate a decision support index which is capable of predicting the lifetime revenue of animal for harvest taking cognisance of both additive and non-additive genetic effects as well as contributing non-genetic effects. Such an index has the potential to be targeted towards beef-finishing systems to aid in the purchase of animals destined for slaughter but also for better aligning animals to different production and finishing systems; with modifications, the index could also be used by beef processors when agreeing flat prices for cattle prior to slaughter.

4.3 Materials and Methods

Data used in the present study were collected prior to October 2018 and originated from the Irish Cattle Breeding Federation (ICBF) national database, Bandon, Co. Cork, Ireland (http://www.icbf.com).

4.3.1 Data

Three separate phenotypic datasets used in the Irish national genetic evaluations were obtained from the ICBF. The first dataset contained calving performance phenotypes on 20,847,261 individual animals for calf mortality, gestation length and calving difficulty; the associated pedigree file included 25,504,740 animals. The second dataset contained docility performance phenotypes on 3,012,970 individual animals, which were either scored subjectively by the farmer or by a trained professional; the associated pedigree file included 6,163,517 animals. The third dataset contained data on 24 traits, namely those related to feed intake, live-weight and carcass-related related traits on 13,126,903 individual animals; the associated pedigree file included 18,078,810 animals. The phenotypes in the performance data included live-weight measurements taken at three life-stage points, namely between the ages 150 d and 250 d old (weanlings), between 251 d and 350 d old (adolescent), between 351 d and 450 d old (adult), and between 451 d and 550 d old (finisher). The three datasets represent the three suites of multi-breed multi-trait genetic evaluations undertaken in Ireland to derive estimated breeding values (EBVs) for calving performance, docility and carcass merit. Heterosis and recombination coefficients were available for all animals, estimated using the methodology reported by VanRaden and Sanders (2003). Depending on the genetic evaluation, either a general heterosis coefficient per animal was available or a heterosis coefficient to represent beef × beef and beef × dairy parents. Heterosis coefficients were available for the animal itself and its dam.

4.3.2 Genetic Evaluations

Genetic evaluations were run for the three suites of traits using the MiX99 software suite (MiX99 Development Team, 2015) to generate both fixed and random effect solutions for all traits included in the Irish beef cattle Terminal index. The carcass genetic evaluation was a 24 × 24 multi-trait evaluation. Fixed and random effect solutions for carcass weight, carcass conformation (i.e., the muscularity score of the carcass; Englishby et al., 2016) , carcass fat (i.e., subcutaneous fat cover and fat in the thoracic cavity; Englishby et al., 2016), feed intake as well as all live-weight age categories were generated for use in the present study. The docility genetic evaluation was a 3 × 3 multi-trait evaluation which included the traits weanling docility assessed by producers or trained professionals, separately, and producer-scored docility of the dam; only the producer-scored weanling docility fixed and random effects solutions were retained for use in the present study as this is the trait included in the national terminal index. Although the calving genetic evaluation was a 9 × 9 multi-trait evaluation, only random effect solutions were retained for a subset of the three relevant traits, namely calving mortality, calving difficulty and gestation length. The statistical models used in the respective genetic evaluations are summarised in Supplementary Material S9.1.

4.3.3 Production value estimation

Genetic evaluations in Ireland use genetic groups (stratified by breed) for the estimation of breed effects. In the present study, however, breeds were fitted as separate covariates. This facilitated the estimation of animal total merit for a given trait using three alternative formulations as follows: 1) using just the breed effect solutions, 2) using the animal's additive genetic merit combined with the breed effect solutions (EBV) and, 3) to estimate an animal's production value (PV) using the fixed and random solution coefficients from the respective genetic evaluations. The PVs were calculated as:

$$Carcass\ traits\ PV_{cdefghz} = \sum_{a=1}^{4} b_1 Het_z + \sum_{b=1}^{16} b_2 Breed_z + EBV_{cz} + b_3 Twin_{dz} + b_4 DamDfract_{ez} + b_5 Dam\ age_{fz} | Dam\ parity_{gz} + DamPe_{hz}$$

$$Feed\ Intake\ PV_{cdefg} = \sum_{a=1}^{4} b_1 Het + \sum_{b=1}^{16} b_2 Breed + EBV_c + b_3 Twin_d + b_4 DamDfract_e + b_5 Dam\ age_f | Dam\ parity_g$$

$$Docility\ PV_{acgij} = b_1 Het_a + \sum_{b=1}^{16} b_2 Breed + EBV_c + b_3 Dam\ parity_g + b_4 Sex_i + b_5 Recomb_j$$

where $Carcass\ traits\ PV$ = the production values pertaining to carcass traits (subscript z) for weight, conformation and fat; $Feed\ Intake\ PV$ = the production value for feed intake; $Docility\ PV$ = the production value for docility; Het = the heterosis coefficient which is fitted as four separate heterosis coefficients to represent different breed crosses within the carcass trait and feed intake genetic evaluation and is fitted as a single coefficient a in the docility genetic evaluation; $Breed$ = covariate representing the proportion of 16 breeds (i.e., Aberdeen Angus (AA), Aubrac (AU), Blonde D'Aquitaine (BA), Belgian Blue (BB), Charolais (CH), Friesian (FR), Hereford (HE), Holstein (HO), Jersey (JE), Limousin (LM), Piemontese (PI), Montbelliarde (MO), Parthenais (PT), Salers (SA), Shorthorn (SH) and Simmental (SI); EBV_c = the estimated breeding value; $twin_d$ = whether or not the animal was a twin (coefficient d); $DamDfract_e$ = dam dairy-breed proportion coefficient e; $Dam\ age_f | Dam\ parity_g$= the interaction between dam age f and the dam's gth parity (i.e., parity 1 to 7, inclusive) for the carcass traits and feed intake or just the dams gth parity for docility; $DamPe_h$= the maternal permanent environment effect of h; Sex_i = whether the animal was male or female, coefficient i; $Recomb_j$ = recombination coefficient j; $b1$-$b5$ = the associated regression coefficients from the respective national genetic evaluation.

4.3.4 Index development

The Irish national beef terminal index comprises 8 traits including three calving traits (i.e., difficulty, gestation length and mortality), feed intake, docility and three carcass traits (i.e., carcass weight, carcass conformation and carcass fat) (Table 4.1); this index, populated with the relevant EBVs, was used as the base scenario from which two additional variants of the index were compared. The economic weights applied (Table 4.1) were the same for all three indexes evaluated in the present study. The two novel indexes proposed in the present study were:

1. The Calf index - developed to provide support in purchasing young animals to be reared and eventually harvested. The Calf index comprised 5 traits namely docility,

feed intake, carcass weight, carcass conformation and carcass fat (Table 4.1); therefore the index did not incorporate calving-related traits.

2. The Harvest index was an adaption of the Calf index in that feed intake and docility were omitted leaving only the three carcass-related traits, namely carcass weight, carcass conformation, carcass fat (Table 4.1).

Table 4.1: Component traits of the different indexes evaluated, including the traits units of measurement, genetic standard deviation (SD) and economic weighting.

	Index					
Component trait	National Terminal	Calf	Harvest	Units	Genetic SD	Economic weight
Calving difficulty	✓	-	-	%	0.158	-€4.65
Calving mortality	✓	-	-	0 to 1	0.038	-€5.34
Gestation length	✓	-	-	Days	3.020	-€2.25
Docility[1]	✓	✓	-	1 to 5	0.365	€17.03
Feed intake	✓	✓	-	kg DM per day	0.667	-€38.63
Carcass weight	✓	✓	✓	Kg	15.419	€3.14
Carcass Conformation[2]	✓	✓	✓	EUROP scale	0.644	€14.77
Carcass Fat[3]	✓	✓	✓	1 to 15	0.679	-€7.86

[1] Where 1 = very quiet and 5 = very difficult,
[2] Where E (best) to P (worst),
[3] Where 1 = leanest and 15 = fattest

4.3.5 Index Validation

A subset of animals from the national beef bull performance test centre at Tully, Co. Kildare, Ireland, were identified to validate each of the constructed indexes. The validation population consisted of 374 steers and 500 young bulls that were slaughtered between the years 2016 to 2018, inclusive; therefore, phenotypic data for carcass weight, carcass conformation, and carcass fat as well as feed intake were available. Details on the test protocols (e.g., diet) and the feed intake phenotypes have been described in detail by Crowley et al. (2010) and Kelly et al. (2019).

Price (€) per kg of carcass weight was determined using the EUROP beef classification grid scores (Englishby et al., 2016) to reflect the current pricing structure used by abattoirs throughout Ireland; the price per kg for different carcass conformation score by fat score credentials are summarised in Supplementary Table S9.4. To generate the animal's carcass value, price per kg was multiplied by their carcass weight. The carcass genetic evaluations were rerun seven times while the docility genetic evaluation was rerun twice to reflect the scenario where additional information (e.g. live-weight phenotypes) becomes available as the animal grows; all phenotypic records belonging to all other animals not pertaining to the validation population were also included in each genetic evaluation iteration. The first iteration of the carcass and docility national genetic evaluations contained all phenotypes of the validation animals to determine the upper threshold of predictive ability. In the next iteration, all phenotypic data of the validation animals were masked in both the carcass and docility national genetic evaluations and the fixed and random effects model solutions re-estimated. For the third, fourth, fifth and sixth iteration of the carcass national genetic evaluations, a single live-weight record of the validation animals was included separately for the age category 150 d up to 250 d (n = 168), 250 d up to 350 d (n = 459), 350 d up to 450 d up (n = 459) or 450 d up to 550 days (n = 459), respectively (Supplementary Table S9.5). For the final iteration of the national carcass genetic evaluation, the phenotypes of animals within the validation population who had a live-weight record for each of the three age categories that spanned from 250 d to 550 d were included (n = 459).

4.3.6 Statistical analyses

Animals were ranked into four strata of equal sizes separately based on their national Terminal, Calf or Harvest index value. The mean Irish national Terminal, Calf and Harvest index values of the animals within the top and bottom 25 % strata were calculated. Least square means (LSM) were calculated for the three carcass traits (i.e., weight, conformation and fat), feed intake, carcass revenue, price per kg and age at slaughter whilst adjusting for the following: 1) gender (i.e., steer or young bull), 2) age at slaughter (with exception to age at slaughter), 3) heterosis, 4) dam heterosis, 5) dam parity and, 6) carcass weight (only included when estimating the least squares means for age at slaughter). Spearman correlations were used to estimate within-gender correlations but also partial correlations adjusted for gender. Spearman correlations between each phenotypic value as well as carcass revenue and price per kg with the whole range of different indexes and scenarios evaluated were estimated. The statistical test proposed by Steiger (1980) was used to test the difference between the correlation coefficients. The statistical test proposed by Steiger (1980) was used to test the difference between the correlation coefficients. Multiple linear regression models in the validation animals were used to regress the phenotypes for carcass weight, carcass conformation, carcass fat score, feed intake, and docility on the three alternative definitions of an individual animal's total merit for a given trait using the models:

$$Carcass\ traits_{abcd} = \sum_{a=1}^{2} HY_a + \ gender_b + \sum_{\mathrm{c}=1}^{3} \mathrm{age}^{c} \ + TM_d + e$$

$$Feed\ intake_{ebcd} = \ HYSfi_e + \ gender_b + \sum_{\mathrm{c}=1}^{3} \mathrm{age}^{c} \ + TM_d \ + e$$

$$Docility_{fbcd} = \ HYSdoc_f + \ gender_b + \sum_{\mathrm{c}=1}^{2} \mathrm{age}^{c} + TM_d + e$$

where HY_a = the class effect of herd-year contemporary group of slaughter and the previous herd in which the animal spent the longest time in; $HYSfi_e$= the class effect of herd-year-season contemporary group of the feed intake; $HYSdoc_f$ = the class effect of herd-year-season contemporary group of docility; $gender_b$ = fitted as a class effect whether the animal a steer or a young bull; age^{c} = the age of the animal (linear, cubic and quadratic for the three carcass traits and feed intake and linear and cubic for docility); TM_d = the total merit estimate; *e* = residual.

4.4 Results

The mean performance of animals ranked on their national beef terminal, Calf, and Harvest index values is in Table 4.2. Although not always significant (i.e., P > 0.05), the mean performance of the bottom 25 % of animals tended to get progressively worse shifting from ranking on the terminal index to ranking on the Calf index and from the Calf index to the Harvest index; similarly, the mean performance of the top 25 % of animals tended to get better shifting from using the terminal index to rank animals versus using the Calf index and from using the Calf index to using the Harvest index. The carcass value of the top 25% of animals ranked on the Harvest index was superior ($P < 0.05$) to that of the top 25 % ranked on the terminal index. This was predominantly due to the heavier ($P < 0.05$) carcass weight of the top 25 % of animal ranked on the Harvest index relative to the top 25 % ranked on the terminal index.

Table 4.2: The mean index value, least square means and standard error (within parenthesis) of animals within the top and bottom 25% when ranked on their Irish national Terminal (Terminal), Calf and Harvest index values, separately.

		Means (SE)		
Trait	Rank	Terminal	Calf	Harvest
Index Value (€)	Bottom 25 %	103.24 (2.47)^{a}	232.30 (2.92)^{b}	254.16 (2.93)^{c}
	Top 25 %	246.92 (1.32)^{a}	406.70 (1.67)^{b}	408.76 (1.66)^{b}
Carcass revenue (€)	Bottom 25 %	1497 (13.35)^{a}	1483 (12.81)^{a}	1463 (12.48)^{a}
	Top 25 %	1688 (13.20)^{a}	1716 (12.87)^{a}	1723 (12.26)^{a}
Price per kg (kg)	Bottom 25 %	4.07 (0.01)^{a}	4.07 (0.01)^{a}	4.07 (0.01)^{a}
	Top 25 %	4.19 (0.01)^{a}	4.19 (0.01)^{a}	4.18 (0.01)^{a}
Carcass weight (kg)	Bottom 25 %	366.95 (2.94)^{a}	363.73 (2.83)^{ab}	358.63 (2.75)^{b}
	Top 25 %	401.75 (2.91)^{a}	408.62 (2.85)^{ab}	411.15 (2.70)^{b}
Carcass conformation (EUROP scale)	Bottom 25 %	9.28 (0.09)^{a}	9.24 (0.09)^{a}	9.27 (0.09)^{a}
	Top 25 %	11.21 (0.09)^{a}	11.19 (0.09)^{a}	11.04 (0.09)^{a}
Carcass fat (1 leanest to 15 fattest)	Bottom 25 %	7.39 (0.09)^{a}	7.34 (0.09)^{a}	7.25 (0.09)^{a}
	Top 25 %	6.00 (0.08)^{a}	6.00 (0.09)^{a}	6.14 (0.09)^{a}
Feed intake (kg DM)	Bottom 25 %	13.31 (0.11)^{a}	13.37 (0.11)^{a}	13.21 (0.11)^{a}
	Top 25 %	12.57 (0.11)^{a}	12.55 (0.11)^{a}	12.89 (0.11)^{b}
Age at slaughter (d)	Bottom 25 %	572.61 (4.18)^{a}	576.34 (4.16)^{ab}	586.90 (4.04)^{b}
	Top 25 %	545.71 (4.14)^{a}	541.09 (4.22)^{a}	534.86 (4.09)^{a}

Different superscripts across the indexes for each trait indicate a difference ($p < 0.05$)

4.4.1 Relationships with phenotypic performance

The correlations between the alternative formulations of total merit of an individual animal for a given trait and the corresponding phenotypic values for that trait are in Table 4.3. As more information was included in the calculation of the total merit (i.e., from just breed effects to inter- and intra-breed effects, to then also include non-genetic effects), the partial correlations between the estimate of total merit for a given trait and the respective phenotypic value typically strengthened. The correlations between the estimate of total merit for a given trait using just breed solutions and the corresponding phenotypic values were consistently weaker ($P < 0.05$) relative to when the total merit estimate included inter- and intra-breed effects, as well as when including non-genetic effects (with exception to feed intake and the within steer group for carcass fat). Furthermore, the correlations between the phenotypic values for both carcass fat and carcass weight (with the exception of the young bull group) and the relative total merit formulated using PVs were stronger ($P < 0.05$) compared to when formulating the total merit using just EBVs.

The regression coefficients of the phenotypic value for all five traits on the three formulations defining an individual's total merit for that trait after accounting for age, sex and contemporary group effects are in Table 4.3. With the exception of carcass weight and feed intake, the regression coefficient was always closer to 1 for the total merit derived using PVs relative to the total merit estimated using just breed, although it not always different to when the total merit was estimated from just EBVs. With the exception of feed intake, the least amount of variation explained by the multiple linear regression model was when total merit was defined solely on breed effects (ranging from 49% (docility) to 72% (carcass conformation)) relative to EBV or PV estimates; irrespective of whether the total merit for feed intake was based on just breed or PV, the regression models explained 53% of the variation.

Table 4.3: Partial and within-sex correlations between the three formulations of an individual's total merit (i.e., just breed effects (Breed), inter- and intra-breed effects (EBV) or production value estimates (PV)) for a given trait and the corresponding realised phenotypic values for the trait. Regression coefficients, standard errors (within parenthesis), and coefficient of determination of each trait's phenotype regressed on the respective three variant estimates.

		Correlations				
Trait	Total merit	Partial (n=874)	Steer (n=374)	Young bull (n=500)	Regression (n=874)	R^2
Carcass weight	Breed	0.16^{a}	0.03^{a}	0.26^{a}	0.94 (0.24)	0.64
	EBV	0.36^{b}	0.33^{b}	0.40^{b}	1.27 (0.09)	0.7
	PV	0.40^{c}	0.40^{c}	0.42^{b}	1.26 (0.09)	0.72
Carcass conformation	Breed	0.51^{a}	0.55^{a}	0.49^{a}	1.20 (0.09)	0.72
	EBV	0.64^{b}	0.65^{b}	0.66^{b}	1.09 (0.05)	0.78
	PV	0.64^{b}	0.66^{b}	0.66^{b}	1.09 (0.05)	0.78
Carcass fat	Breed	0.40^{a}	0.46^{ab}	0.37^{a}	1.14 (0.12)	0.61
	EBV	0.42^{a}	0.44^{b}	0.44^{b}	1.10 (0.09)	0.64
	PV	0.47^{b}	0.47^{a}	0.49^{c}	1.03 (0.08)	0.65
Feed Intake	Breed	0.35^{a}	0.38^{a}	0.35^{a}	1.08 (0.10)	0.53
	EBV	0.37^{a}	0.40^{a}	0.35^{a}	0.84 (0.08)	0.52
	PV	0.38^{a}	0.42^{a}	0.36^{a}	0.83 (0.08)	0.53
		Partial (n=438)	Steer (n=122)	Young bull (n=316)	Regression (n=438)	
Docility	Breed	-0.01^{a}	0.00^{a}	-0.01^{a}	1.61 (0.73)	0.49
	EBV	0.14^{b}	0.15^{b}	0.14^{b}	0.67 (0.16)	0.51
	PV	0.14^{b}	0.14^{b}	0.15^{b}	0.67 (0.16)	0.51

Different superscripts across the indexes for each trait indicate a difference ($p < 0.05$)

The partial correlations between the three indexes and their different constructions with each of the phenotypic values for the component traits are in Table 4.4. Regardless of the index, or how it was formulated (i.e., breed effects only, EBV, or PV), there was little to no relationship between either of the indexes and docility, with correlations ranging from -0.04 (the Calf index calculated using only breed solutions) to 0.05 (the Harvest index calculated using the EBV solutions). Irrespective of the formulation of the three indexes, phenotypic carcass fat and feed intake were both negatively correlated (i.e., the desired direction) with each of the three indexes (from -0.45 to -0.35 and from

-0.39 to -0.09 for carcass fat and feed intake, respectively; Table 4.4). Of all the traits, carcass conformation was the most strongly correlated with each of the indexes evaluated.

Table 4.4: Partial correlations between three indexes calculated using formulations of an individual’s total merit (i.e., calculated using just breed effects (Breed), inter- and intra-breed effects (EBV) or production value estimates (PV)) and the realised phenotypic values for the three carcass traits (weight, conformation and fat), feed intake and docility.

Indexes	Sub-components	Carcass weight (n = 874)	Carcass conformation (n = 874)	Carcass fat (n = 874)	Feed intake (n = 874)	Docility (n = 438)
Terminal	EBV	0.21	0.53	-0.43	-0.24	0.01
Calf	Breed	0.12^{a}	0.49^{a}	-0.44^{ab}	-0.39^{a}	-0.04^{a}
	EBV	0.29^{b}	0.57^{b}	-0.44^{a}	-0.25^{b}	0.02^{b}
	PV	0.33^{c}	0.56^{b}	-0.40^{b}	-0.22^{c}	0.00^{ab}
Harvest	Breed	0.15^{a}	0.49^{ab}	-0.45^{a}	-0.35^{a}	-0.01^{ab}
	EBV	0.35^{b}	0.53^{a}	-0.39^{b}	-0.12^{b}	0.05^{a}
	PV	0.39^{c}	0.50^{b}	-0.35^{c}	-0.09^{c}	0.02^{b}

[1]n = number of animals included in analysis
Different superscripts between the three different formulations of the indexes for each trait separately indicate a difference ($p < 0.05$)

4.4.2 Correlations with revenue metrics

The correlations between each of the three indexes with both the total carcass value and price per kg are in Table 4.5. The national terminal (breeding) index, which is the Irish industry standard for beef breeding, was moderately correlated with carcass value and price per kg. For the Calf index, the correlations with carcass value strengthened as more information was included in the calculation of the index ($P < 0.05$); the same was true for the Harvest index ($P < 0.05$; with the exception of in young bulls). In fact, the strength of the correlations almost doubled ($P < 0.05$) when either index was formulated using PVs compared to when it was formulated using just breed effects. The strongest correlations were between price per kg and the Calf index when formulated on either EBVs or PVs relative to using just breed solutions ($P < 0.05$). The correlations were strongest between price/kg and the Harvest index formulated using EBVs relative to the index calculated using PVs ($P < 0.05$).

4.4.3 Including live-weight data in the genetic evaluations

The partial correlations between the three indexes with the carcass revenue as the number of live-weight records available for each individual included in the genetic evaluation changed are in Table 4.6. Where no live-weight records were included in the genetic evaluations, partial correlations between the indexes and carcass value followed the same trend (i.e., strengthened as more information was included in the calculation of the index; $P < 0.05$) as described in Table 4.5, albeit with a small number of animals included. The correlations between the national terminal index and carcass value strengthened ($P < 0.05$) from 0.30 to 0.36 with the inclusion of one live-weight phenotype recorded between 250 to 450 d of age; the correlation further strengthened ($P < 0.05$) to 0.39 if the live-weight included in the genetic evaluation was recorded between 450 to 550 d of age. Partial correlations were either 0.18 between carcass value and Calf index or 0.23 between the Harvest index and carcass value regardless of the number of live-weight records included in the genetic evaluation, provided the indexes were formulated using just breed solutions. In comparison to when no live-weight phenotypic data on the validation animals were included in the genetic evaluation, the inclusion of one live-weight record strengthened ($P < 0.05$) the correlations between carcass value and both the Calf and Harvest index formulated using PVs or EBVs; between the ages of 250 to 450 d, the correlations did not differ (i.e., $P > 0.05$) regardless of when the live-weights were recorded or indeed the number of live-weight phenotypes included in the genetic evaluation (with exception to the Harvest index). When only including one live-weight record in the genetic evaluation, the strongest correlations ($P < 0.05$) existed between the Calf index formulated using PVs and the carcass value when the live-weight of an older animal was included (450 to 550 d of age); the same was true for the Harvest index ($P < 0.05$). Provided there was an older animal's live-weight record included in the genetic evaluation, there was no further benefit to the inclusion of multiple live-weight records.

Table 4.5: Partial and within-sex correlations between the three indexes calculated using formulations of an individual's total merit (i.e., just breed effects (Breed), inter- and intra-breed effects (EBV) or production value estimates (PV)) and the realised quality pricing carcass value as well as the price/kg based on the quality pricing grid payment structure common to Ireland where n = number of animals.

		Quality Pricing Carcass Value			Price/kg		
Indexes	Sub-components	Partial (n=874)	Steer (n=374)	Young bull (n=500)	Partial (n=874)	Steer (n=374)	Young bull (n=500)
Terminal	EBV	0.29	0.29	0.32	0.54	0.63	0.51
Calf	Breed	0.20^{a}	0.18^{a}	0.22^{a}	0.50^{a}	0.58^{a}	0.46^{a}
	EBV	0.36^{b}	0.35^{b}	0.42^{b}	0.58^{b}	0.65^{b}	0.57^{b}
	PV	0.40^{c}	0.38^{c}	0.45^{c}	0.57^{b}	0.64^{b}	0.55^{b}
Harvest	Breed	0.22^{a}	0.15^{a}	0.29^{a}	0.50^{ab}	0.58^{ab}	0.48^{ab}
	EBV	0.41^{b}	0.40^{b}	0.48^{b}	0.53^{a}	0.62^{a}	0.51^{a}
	PV	0.44^{c}	0.44^{c}	0.49^{b}	0.50^{b}	0.60^{b}	0.48^{b}

Different superscripts between the three different formulations of the indexes for each trait separately indicate a difference ($p < 0.05$)

Table 4.6: Partial correlations across a sub-set of 459 validation animals between the three indexes constructed using formulations of an individual's total merit (i.e., just breed effects (Breed), inter- and intra-breed effects (EBV) or production value estimates (PV)) and the realised quality pricing carcass value; n = number of live-weight phenotype records taken at each specific time points included in each genetic evaluation iteration.

			250-349 d	350-449 d	450-549 d	250-449 d	250-549 d
Indexes	Sub-components	(n = 0)	(n = 1)	(n = 1)	(n = 1)	(n = 2)	(n = 3)
Terminal	EBV	0.30^{a}	0.36^{b}	0.36^{bc}	0.39^{d}	0.37^{c}	0.39^{d}
Calf	Breed	0.18^{a}	0.18^{a}	0.18^{a}	0.18^{a}	0.18^{a}	0.18^{a}
	EBV	0.38^{a}	0.44^{b}	0.43^{bc}	0.46^{de}	0.44^{cd}	0.46^{e}
	PV	0.41^{a}	0.46^{b}	0.46^{bc}	0.49^{d}	0.47^{c}	0.49^{e}
Harvest	Breed	0.23^{a}	0.23^{a}	0.23^{a}	0.23^{a}	0.23^{a}	0.23^{a}
	EBV	0.47^{a}	0.54^{b}	0.55^{b}	0.58^{c}	0.56^{d}	0.59^{c}
	PV	0.51^{a}	0.57^{b}	0.58^{b}	0.61^{c}	0.59^{d}	0.62^{c}

Different superscripts, within row, indicate a difference ($p < 0.05$) between the correlation coefficients within that row

4.1 Discussion

The main revenue source for beef producers is carcass value, which is a function of both carcass price and carcass weight; carcass price itself is a function of the carcass conformation and fat grade. Almost a quarter of a million calves are sold younger than 6 weeks of age at Irish livestock auctions annually, with a further quarter million sold younger than 12 months of age (DAFM, 2018a); combined this represents almost 40% of the prime animals that are eventually harvested. Thus the ability of producers to predict the future carcass value of an animal at sale can be extremely difficult due to many of the animals being sold at such a young age relative to their age at harvest (approximately 730 days old; Berry et al. 2017). Hence, the motivation for the present study was to develop a tool that could predict an animal's potential carcass value and therefore aid in the decision-making process when purchasing animals; this was particularly true where the animal was young and thus the visible expression of genetic differences in weight and conformation is expected to be poor.

In doing so, the aim of the present study was also to determine whether there was a benefit from taking cognisance of not only the within-breed additive genetic merit of an individual, but also the non-additive genetic and non-genetic effects, both of which are known to contribute to the eventual carcass phenotype (Connolly et al., 2016). Nonetheless, a caveat in estimating an animal's future carcass value using *a priori* predictions, especially at such a young age, is that such predictions will never be extremely accurate due to the number of factors that are associated with differences in carcass value, some of which will not be known at the time of prediction. For instance, not only does age at harvest have a big impact of carcass performance (Judge et al., 2019), but also whether the animal will be finished as a bull or steer (Connolly et al., 2016). Thus, the carcass value predictions from the two proposed indexes are simply to assist in comparing candidate animals for purchase rather than an absolute prediction of carcass value *per se*.

4.1.1 Why not just use a breeding index in the transaction of animals?

Subjective evaluation of an animal's visible characteristics, and their likely association with animal value, has been fundamental to livestock improvement since the beginning of livestock domestication (Cole and VanRaden, 2018). A general feeling among some is that knowledge of the breed (combinations) of an animal is sufficient to predict its future carcass merit. In fact, whilst investigating the between-breed differences of 15 European cattle breeds, Albertí et al. (2008) suggested that, within reason, carcass weight and dressing percentage is largely reflected by breed type. For this reason, the present study investigated the relationship between the 5 performance phenotypes and just the breed solutions of an animal. Although positive correlations did exist between the trait phenotypes and the respective total merit based on just breed solutions (with the exception of docility; Table 4.3), exploiting the known within-breed variability in EBVs and non-genetic effects (i.e., the PVs) improved the partial correlation prediction accuracy by 0.09 (feed intake) to 14 (docility) times that of using the breed solutions alone. It is currently a legal requirement to record the breed of all animals in Ireland. Thus, it is possible to estimate the within-breed genetic potential of an animal over and above the breed effects. This is especially true given the growing uptake of genotyping in cattle (Wiggans et al., 2017) which improves the ability to not only predict animal breed composition more accurately (Judge et al., 2017), but can also (in)validate parentage (Purfield et al., 2015) on a greater number of (commercial) animals, thus improving the precision of prediction.

Animals excelling in the terminal index have been documented to produce, on average, heavier, more conformed carcasses when compared to their lower genetic merit contemporaries (Connolly et al., 2016). Despite this, as calving performance-related traits (i.e., dystocia, gestation length and calf mortality) represent approximately 25 % to 50 % of the relative emphasis within the terminal indexes, it is possible that animals of potentially superior carcass merit will be penalised owing to their expected poorer calving performance. This is because of the known positive genetic correlations between calving difficulty and carcass weight in cattle (Berry et al., 2019a), as well as between calf birth weight and calving difficulty (Eriksson et al., 2004). However, when purchasing calves or weanlings solely for eventual harvest, it is not logical to consider an individual's merit for calving traits (since the animal is already born). This prompted the development of both the Calf and Harvest indexes in the present study to satisfy the void in decision support tools for the transaction of animals for harvest, or in other words, those that will never become parents.

The Irish national terminal breeding indexes, like all other cattle indexes globally are solely based on the individual animal's additive genetic merit for the component traits. This in part is not only due to the difficulty in estimating non-additive genetic effects (Bolormaa et al., 2015), but also that the expression of non-additive genetic effects of a bull is a function of (the genotype of) its mate. Nevertheless, using genotypic and phenotypic data from beef cattle, Bolormaa et al. (2015) estimated that 10 % and 18 % of phenotypic variance for intra-muscular fat (i.e., marbling) and carcass retail beef yield (i.e., saleable beef yield; kg), respectively, was explained by dominance variance. As the non-additive genetic merit of an animal can be theoretically estimated once born (Bolormaa et al. (2015); dominance variance), it makes sense to consider this influence in the prediction of performance. This is especially true given that the prediction of carcass value improved once the non-additive and non-genetic effects were considered in the total merit estimation (i.e., PVs; Table 4.5).

4.1.2 Index deployment

In its simplest form, the index published for an animal could graduate from being the terminal index value (includes calving performance) at the national genetic evaluation immediately post conception, to the Calf index coinciding with the first national genetic evaluation after the birth of the animal. As the Harvest index is targeted towards older animals, to avoid confusion it would be more beneficial for it to be published as the animal nears the expected harvest date. A shortcoming of the proposed indexes within the present study is the number of traits considered is limited, which here is simply a function of the data available for genetic evaluations. The economic weights applied to each trait used in the present study were the same for all indexes and were those from the Irish breeding indexes which are based on current day costs and prices. Greater certainty on carcass value may exist when purchasing an animal to be harvested in the very near future. In such a case, for deployment, the economic values used in the decision support tool could be more dynamic, linked to projected costs and values; the economic values used could even differ by index or the time horizon until projected slaughter date which could also be used to account for known seasonal variability in prices and costs.

Given the accelerating developments in the internet of things, animal level sensors for measuring different characteristics (Johnsen et al., 2019; colostrum immunoglobulin (IgG) in saliva), biomarkers for growth (Ibeagha-Awemu and Zhao, 2015; epigenetics), as well as the associated systems for traceability like blockchain (Makhdoom et al., 2018), there is massive potential to improve, not only the dynamic nature of the indexes, but also the completeness and validity of the data contributing to the index values. While one of the current limitations of the present study is the incorporation of only a few traits in the overall index, there is also a reliance on producers to accurately record the data (e.g. calving difficulty score) in order to provide reliable estimates. Blockchain technology offers the potential to include considerably more traits (e.g., animal health and remedies administered) and, in doing so, offers a system to ensure data integrity, thus improving the credibility of the data used in the evaluations. Such data could include information on the animal that spans from their healthcare history to movements, thus providing a full traceability report that can be verified by the different peers. The two proposed indexes have the capability of utilising more information and being integrated into IoT systems to provide updated predictions of carcass value and details of provenance as the uptake in the technology intensifies.

The benefit of including a single live-weight phenotype in the genetic evaluation for improving the accuracy of predicting carcass value was clear (Table 4.6), although the benefit of additional live-weight records was minimal; the relatively low return in prediction accuracy with additional live-weight records is most likely due to the high heritability of live-weight in cattle coupled with the strong genetic correlation that exists among live-weight records at different life-stages (McHugh et al., 2011). Live-weight phenotypes are often recorded at livestock auctions in Ireland immediately prior to slaughter. These information sources could be integrated via selection index methodology into the final index estimate of an animal, much like the ad hoc blending approach used in two-step genomic evaluations (e.g., VanRaden et al., 2019).

Linking IoT with application programming interfaces (APIs) could provide an excellent route to market for such an index. Several hundred animals can be traded in livestock marts on a given day. These animals are usually booked in the day before. Prospective purchasers of cattle could download all registered animal details the day before the sale onto their mobile devices. Animals could be filtered for personal preferences such as breed type, genotype status or age. Using the animal RFID tags, those on the filtered list could then be visually inspected the following day and their respective transaction index studied. Another possibility entirely could be the introduction of a brokerage system, whereby an intermediate party could link potential sellers to buyers and *vice versa* based on their criteria, without the animals needing to visit an intermediary location. This direct farm-to-farm movement would minimise the stress on animals with obvious welfare and biosecurity benefits as well as potential cost savings for both parties in the transaction.

4.2 Conclusions

The Calf and Harvest indexes proposed in the present study are a simple evolution of existing selection indexes by 1) focusing on just the traits pertinent to the live animals, 2) including non-additive genetic effects in the prediction of total genetic merit and 3) including also relevant (and available) non-genetic effects in the prediction of eventual carcass value. A simplistic approach to incorporate inter-animal differences in the cost of production was also demonstrated. The end result of such developments is a more accurate prediction of eventual carcass value. Inclusion of live-weight data on the animal itself also improves the accuracy of prediction thus providing an incentive for recording data.

Chapter 5: An index framework founded on the future profit potential of beef females as a tool to support the identification of animals for retention and culling

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5.1 Abstract

Meticulous culling decisions, coupled with careful breeding decisions, are fundamental to shifting the distribution in the favourable direction and improving the profit per cow. While cattle breeding indexes are ubiquitous, there is a paucity of easy-to-use dynamic tools to aid in culling decisions in beef cattle. Building such a culling tool on the framework of breeding indexes can expedite their uptake given the familiarity of the end user with the approach. The motivation for the present study was to develop a culling tool, complementary to a currently available breeding index, to identify females for culling. The monetary-based culling index, here referred to as the Beef Female's Profit Potential (BFPP), reflects the expected lifetime profitability of every individual female in a herd for the expected remainder of her lifetime; this profit included that of the cow herself as well as her progeny destined as both replacement females or for harvesting. The framework of the culling index was composed of four sub-indexes reflecting the value of an animal 1) as a nulliparae (this was voided if the cow had already calved), 2) for the remainder of her current parity, 3) summed across each of her expected remaining parities, and 4) when she is retained within the herd and not voluntarily culled. Each sub-index was comprised of different components reflecting both additive genetic, non-additive genetic and non-genetic effects associated with each female. Many of these effects were generated from readily available fixed and random effect solutions from routine genetic evaluations. Transition matrices depicting the expected longevity of each female and their expected month of calving were also utilised in calculating the expected remaining lifetime profitability of each female. The BFPP index was validated by stratifying, within herd, cows into four strata on their BFPP; the validation population consisted of 21,102 beef cows as well as their harvested progeny from 875 herds. On average, the future parity sub-index of the BFPP had the strongest correlation with the overall BFPP index (r = 0.86). The within-herd correlation between the BFPP and national maternal breeding index was, on average, 0.47 indicating the shortcomings of the breeding index as a culling tool. Cows within the top BFPP stratum had a genetic expectation of accruing an additional €37.46 profit per calving, relative to cows within the worst stratum; when validated on the cows own calving interval and survival performance as well as their progeny's carcass performance, the actual phenotypic value was estimated to be an additional €32.31 profit per calving. A proportion of this additional profit was due to the harvested progeny of the high BFPP

cows having, on average, heavier more conformed carcasses with fat scores relative to their poor BFPP contemporaries. This BFPP framework is a useful and easy-to-understand tool to aid in producer decision making on the choice of females to voluntarily cull but also on which replacement heifers to enter the herd.

5.2 Introduction

Culling decisions in cattle are complex and multifactorial (Bascom and Young, 1998); an inefficient culling strategy will impact the overall profitability of the enterprise (Orpin and Esslemont, 2010). Despite this, the majority of research on culling decisions and implications, as well as the development of decision support tools that support culling decision-making, are almost exclusively for dairy herds (Stewart et al., 1977; Bascom and Young, 1998; Kelleher et al., 2015). Many of the factors impacting voluntary culling decisions are likely to overlap between the dairy and beef sectors such as animal age, health status, and reproductive performance. Nonetheless, not all risk factors for culling in dairy cows are pertinent to beef cows and additional risk factors unique to beef production systems also exist. Crosson et al. (2015) reported that animal performance, in the form of the value of animals sold per beef cow, is one of the main factors contributing to profitability in beef herds. Given the high heritability of carcass weight (Pabiou et al., 2009), conformation (Coyne et al., 2018) and animal value (McHugh et al., 2011) in beef cattle, the cow herself has a large impact on the value of her progeny; hence, the future predicted value of offspring will have a large bearing on whether or not a given beef cow is a candidate for culling. An opportunity therefore exists to develop the framework for a novel decision support tool tailored specifically to the beef sector; this should incorporate chief performance metrics relevant to a beef female reflecting her (future) relative economic worth to the herd. For instance, the ability for a beef female to produce a calf per year at the desired time of year, and her probability of continuing to produce several more quality offspring, are both important key performance indicators. Indicators of milk production reflected in the expected relative weaning weight of her future progeny will impact her contribution to herd profit; maternal weaning weight in cattle is known to be both heritable and repeatable (McHugh et al., 2014). The objective of the present study was to develop the framework for a decision support tool which ranks beef females based on their expected remaining lifetime profit potential. The proposed Beef Female Profit Potential (BFPP) index was developed to be applicable to both heifers and beef cows and therefore incorporates: 1) the animal's potential as a heifer (if she is nulliparous), 2) the remaining profit potential of the cow (provided she has calved at least once) for the current parity, 3) the projected profit potential up to a further 10 parities, and 4) the value of the animal if she was to be retained within the herd and not voluntarily culled. The BFPP was designed to, not only take cognisance of the beef female’s additive genetic merit, but also her non-additive genetic and environmental effects associated with her performance; the outcome is a data-driven support mechanism for producers when making culling decisions.

5.3 Materials and Methods

5.3.1 Model development

The BFPP is intended to be economically-driven decision-support tool developed to rank beef females based on their expected remaining lifetime profit potential. The BFPP framework encompasses four main components of a beef female’s production life: 1) the animal’s heifer profit potential (HP) until she first calves, 2) the cow’s profit potential for the remainder of her current parity (CP), 3) the cow’s future profit potential for her remaining parities (FP) and, 4) the value of the beef female if she is retained within the herd and therefore does not require replacement (RV). The BFPP was therefore calculated as:

$$BFPP = HP + CP + FP + RV \qquad [1]$$

The BFPP represents the beef female’s own performance throughout the (expected) remainder of her lifetime comprised of not only the value she transmits directly to her progeny but also the maternal effects she has on her progeny’s performance and her value herself. Therefore, the beef female’s total merit for each trait was calculated using production values (PVs) in order to accurately reflect her total contribution to each trait; both genetic and non-genetic effects were used in the calculation of PVs. For traits pertaining to the female’s own performance, PVs were calculated using the animal’s estimated breeding value (EBV) for a given trait, her own heterosis value and, where available, the contribution of her permanent environment to her performance; these female traits were: age at first calving (AFC), maintenance (i.e., live-weight), docility, calving interval (CIV), survival and cull cow carcass weight (Table 5.1). For traits pertaining to the beef female’s progeny performance, PVs were calculated using the beef female’s predicted transmitting ability (PTAs, i.e., half the EBV) for the trait of interest, her corresponding maternal heterosis value and, where available, the female’s maternal permanent environmental effect as well as the effect the beef female’s dairy breed fraction has on her progeny’s performance (as per the national genetic evaluation models discussed later); these traits were: progeny carcass traits (i.e., weight, conformation and fat), feed intake, docility and calving related traits (i.e., calving difficulty, mortality and gestation length) (Table 5.1). The statistical models pertaining to the calculation of a beef female's PV for each given trait are described in Supplementary material S1. All fixed and random effect solutions were those estimated for the national genetic evaluations as discussed later. The economic parameters incorporated into the BFPP were obtained from the Grange Beef Model, a mathematical model used to simulate the Irish beef production system (Crosson et al., 2006). As described by Crosson et al. (2006), the model assumes that the beef enterprise is a beef spring-calving (i.e., early March) herd operating on 40 ha and maintaining a predominantly grass-based diet (i.e., grazed grass and grass silage) but extends to concentrates and maize silage, if available. Factors accounted for within the Grange Beef Model include: 1) animal and feeding activities, 2) labour, and 3) environmental considerations.

5.3.1.1 Heifer potential

The heifer potential (*HP*) component of the BFPP was calculated as the estimated profit potential of a beef heifer based on the expected duration until her projected first calving. If the beef female had already had at least one calf when the BFPP was generated, then the HP component of the BFPP was set to 0; otherwise if the female is nulliparous, then the HP component was calculated as:

$$HP = \left(EV_{hafc} \cdot PV_{hafc}\right) \cdot \left(\frac{1}{1+r}\right)^{y} + \frac{y}{2} \cdot \left(\left(EV_{hlwt} \cdot PV_{hlwt}\right) \cdot \left(\frac{1}{1+r}\right)^{y}\right) + \pi \qquad [2]$$

where *HP* is the heifer profit potential component. The economic values (*EV*) relating to heifer traits were calculated based on the time taken from birth to when the trait is expected to be expressed and included heifer age at first calving (*hafc*) and heifer maintenance (*hlwt*) (Table 5.1). The production values (PV) relevant to both heifer traits (i.e., PV_{hafc} and PV_{hlwt}) are described in Table 5.1. A discount factor, $\left(\frac{1}{1+r}\right)^{y}$, with an annual discount rate of 7% (Berry et al., 2006), accounts for the time delay to the expression of the trait where y is the estimated number of years (i.e., y = 1 or 2) until a heifer is predicted to express the trait under consideration. For instance, if a heifer is 1 year old and is expected to express the trait in 1 year's time, then the cost of that trait is halved. A profit differential (π) was added to the HP component to reflect the heifer's predicted month of first calving group (MOCG) which was estimated based on her birth date plus the national average age at first calving for beef heifers which was 950 d (McHugh et al., 2014), and subsequently adjusted based on the heifer's PV for AFC. The profit differential by MOCG was relative to a base female calving in March as described in Table 5.2.

5.3.1.2 Current parity

The current parity (CP) component was calculated as the estimated profit potential accruing from the remainder of the current parity, given the cow's month of calving for that parity. If the beef female for which the BFPP was being generated for was nulliparous, then the CP component was set to 0. The CP component for cows that had at least one calving was calculated as:

$$CP = \sum_{c=1}^{2} EV_c \cdot PV_c + \left((1 - R) \cdot \sum_{t=1}^{5} EV_t \cdot PV_t \right) + R \cdot (RIndex) + \pi \qquad [3]$$

where the economic values (*EV*) are described in Table 5.1 and refer to: 1) cow traits (subscript *c*) represented by the traits cow maintenance and docility, 2) traits relevant to terminal progeny destined for harvesting (subscript *t*) represented by the carcass traits weight, conformation and fat as well as feed intake and calf docility. The associated production values (i.e., PV_c and PV_t) for the cow and terminal progeny traits are described in Table 5.1. The term *R* represents the proportion of females that were assumed to be retained as replacements, which was assumed to be 20%; thus, the remaining proportion of progeny (i.e., $1 - R$) was assumed to be harvested. The replacement index value (*Rindex*) of the beef female's progeny that will be retained within the herd as replacement heifers was expressed as a PTA, in Euros, of profit due to the additive genetic merit of the beef female. The *RIndex* was estimated in line with the current Irish national beef replacement index using PTAs for the 17 traits listed in Table 5.1. Similar to the HP component already described, a profit differential (π), relative to a base female calving in March, was added to the CP component which represented the cow's most recent MOCG (Table 5.2).

Table 5.1: Traits included within the three animal categories (i.e., heifer, cow and terminal progeny) when calculating the heifer potential (HP), current parity (CP), future parities (FP), retention value (RV) and, Replacement index (RIndex) when estimating the Beef Female's Profit Potential index as well as the traits associated economic values (EV).

								Production Value estimation[1]						
								Direct effect[2]			Maternal effect[3]			
Animal category	Trait	HP	CP	FP	RC	RIndex	EV	BV	Het	PE	Het	PE	DFract	Age adj[4]
Heifer	Age at first calving	✓				✓	-€1.61	EBV	✓					
	Maintenance	✓				✓	-€1.24	EBV	✓	✓				
Cow	Maintenance		✓	✓		✓	-€0.25	EBV	✓	✓				
	Cow docility		✓	✓		✓	€35.06	EBV	✓	✓				
	Maternal calving difficulty			✓		✓	-€2.26	EBV			✓	✓		
	Maternal Weaning weight			✓		✓	€2.53	EBV			✓			✓
	Cull cow weight				✓	✓	€3.15	EBV	✓					
	Calving interval			✓		✓	-€2.30	EBV	✓	✓				
	Survival			✓		✓	€4.02	EBV	✓	✓				
Terminal progeny	Calf docility		✓	✓		✓	€18.40	PTA						
	Feed intake		✓	✓		✓	-€0.13	PTA			✓		✓	
	Direct calving difficulty			✓		✓	-€4.65	PTA						
	Direct mortality			✓		✓	-€5.34	PTA			✓	✓		
	Direct gestation length			✓		✓	-€2.25	PTA			✓	✓		
	Carcass weight		✓	✓		✓	€3.89	PTA			✓	✓	✓	
	Carcass conformation		✓	✓		✓	€18.93	PTA			✓	✓	✓	
	Carcass fat		✓	✓		✓	-€10.08	PTA			✓	✓	✓	

[1] Effects included in the estimation of production values

[2] Direct effects included BV= breeding value where EBV = estimated breeding value and PTA = predicted transmitting ability; Het = Beef cow's own heterosis effect, PE = Beef cow's own permanent environmental effect

[3] Maternal effects included: Het = Beef cow's maternal heterosis effect on progeny, PE = Beef cow's maternal permanent environmental effect on progeny, DFract = dam dairy fraction

[4] Age adj = a -17 kg weaning weight EBV adjustment applied to dams who were parity 2 and older so that positive bias did not exist towards older females.

Table 5.2: Net profit margin differential, adjusted to the base month of March, for each month of calving group (MOCG), including the additional dry cow penalty cost (€).

			Additional Dry Cow Penalty (€)[1]		
Predicted and current MOCG			Transition state MOCG		
Group	Name	Net profit differential (€/cow calving)	Jan	Feb and March	April to Aug
1	January	0	-	-	-
2	February	80	-	-	-
3	March	0	-	-	-
4	April	-120	-	-	-
5	May	-210	-399	-474	-649
6	June	-210	-349	-424	-599
7	July and August	-210	-275	-349	-524
8	September	74	-200	-275	-449
9	October to December	-116	-100	-175	-349

[1] Additional dry cow penalty was applied to the transition state month of calving groups 10, 11 and 12 in the fertility transition matrix within the future parity component of the beef female's profit potential index as these capture animals that re-calve two calendar years after their most recent calving

5.3.1.3 Future parity

The future parity (FP) component of the BFPP reflects the estimated profit potential culminated across future projected parities (up to a maximum of 10 additional parities) based on two fundamental transition matrices. Firstly, a survival transition matrix was used to estimate the beef female's probability of surviving and completing her next full parity (i.e., $i*$) and surviving each potential future parity (i.e., i); this was the same approach as used by Kelleher et al. (2015) for dairy cows but populated in the present study with beef cow statistics estimated from the national data (described later). The survival matrix was dependent on the beef female's current MOCG within her current or predicted parity (i.e., x; which was assumed to be parity 1 if she is a nulliparous female) as well her percentile group for survival generated from her PV for survival (i.e., $PG(PV_{SU})$). Secondly, a fertility transition matrix was used to estimate the probability of a beef female calving in the qth MOCG in the subsequent parity ($MOCG_{next_q}$), given her most recent pth MOCG (or predicted MOCG in the case of nulliparae) ($MOCG_p$), and her percentile group for CIV generated from her PV for CIV (i.e.,$PG(PV_{CIV})$). The FP was therefore calculated as:

$$FP = \left(\sum_{j=i*}^{i*+10} \left(\prod_{i=i*-1}^{j-1} P(Survival_i | MOCG, Parity,\ PG(PV_{SU})) \cdot \left(\frac{1}{1+r} \right)^{((j-i^*)+1)\cdot\frac{civ}{365}} \right) \right) \cdot \left(\sum_{c=1}^{4} EV_c \cdot PV_c + \left((1-R) \cdot \sum_{t=1}^{8} EV_t \cdot PV_t \right) + \sum_{q=1}^{11} P\left(MOCG_{next_q} \middle| MOCG_p,\ PG(PV_{CIV}) \right) \cdot \rho + R \cdot (RIndex) \right) \qquad [4]$$

where FP is the future parity component. The term $\sum_{j=i*}^{i*+10}(\prod_{i=i*-1}^{j-1} P(Survival_i | MOCG, Parity,\ PG(PV_{SU}))$ is the sum of the probabilities of the cow surviving to each of the next 10 parities; this would equate to the expected total number of remaining parities to be achieved by the female. A discounting factor, $\left(\frac{1}{1+r}\right)^{((j-i^*)+1)\cdot civ/365}$, penalises each counted parity for the delay between reaching parity *j* and the time of the next full parity plus an additional calving interval (i.e., the average CIV in Ireland in 2019 of 401 days; ICBF (2019a)) assumed to be the time from present until the start of the next full parity in years. The economic values (EV) are described in Table 5.1 and are associated with: 1) cow traits (subscript *c*) represented by cow maintenance, docility as well as the maternal traits of calving difficulty and maternal weaning weight), 2) traits relevant to future terminal progeny destined for harvest (subscript *t*) represented by carcass traits including weight, conformation and fat as well as feed intake, calf docility and direct calving performance traits including calving difficulty, mortality and gestation length. The calculation of the production values (PV) for the cow and terminal traits are described in Table 5.1.

The term $\sum_{j=1}^{11} P\left(MOCG_{next_q}|MOCG_p,\ PG(PV_{CIV})\right) \cdot \rho$ is the summed expected profit associated with the probability of a cow calving in the next MOCG ($MOCG_{next_q}$), given the beef female's current or predicted (i.e., for a nulliparous female) MOCG ($MOCG_p$) and her PV for CIV percentile group ($PG(PV_{CIV})$), where ρ is the profit differential for each current MOCG ($MOCG_p$) plus an additional monetary penalty applied to MOCGs 5 to 9 (i.e., which span from May to December), inclusive, which captured the small probability of animals re-calving two calendar years after their last observed calving event (Table 5.2). This penalty was imposed to reflect the additional cost incurred from retaining a dry cow in the herd and incorporates the costs of additional feed, land and machinery (Supplementary Table S9.6). The terms *R* and *Rindex* are as described previously.

5.3.1.4 Retention Value

The retention value (RV_x) captures the total euro value that is saved if a beef female, who is currently in parity *x*, is not voluntarily culled and is therefore retained within the herd. The RV_x was calculated as:

$$RV_x = RR_x(HRcost - f(Cullwt_x)) \qquad [5]$$

where RR_x is the remaining proportion of the production life of the beef female that would be required to be replaced if she were to be culled at the end of parity *x* (Table 5.3) and therefore accounts for the high replacement cost of voluntarily culling a younger beef female. The $RR_x$was calculated as:

$$RR_x = \left\{ \begin{array}{ll} \dfrac{1 + \sum_{k=x+2}^{10} \prod_{j=x+2}^{k} Pnext_j}{ENP} & when\ 0 \leq x \leq 8 \\ & \\ \dfrac{1}{ENP} & when\ x \geq 9 \end{array} \right\} \qquad [6]$$

where it is assumed that if the beef female was not culled at the end of parity *x*, her probability of starting her next full parity (i.e., i*) would be one (i.e., where 1 is the guaranteed probability of starting parity i* in the numerator of Eq. 6). It is therefore assumed that a nulliparous heifer will start her first parity; however, if the heifer is voluntarily culled prior to her first parity, then RR_x equals 1. The average probability of a beef female surviving her current parity, and therefore starting a subsequent parity, up to parity 10, was captured in the term $Pnext_j$; in the present study, the cow was not assumed to have survived if she did not have a subsequent calving within 600d of her previous calving (taking cognisance of the date of last calving relative to the date of data extraction). The $Pnext_j$ proportions are described in Table 5.3.

Table 5.3: The proportion of animals estimated to survive their current parity and therefore start their next parity (Pnext), the proportion of animals expected to survive their current parity, given their chance of surviving each pervious parity (Psurv) and, the proportion of an animal’s productive life required to be replaced if they were to be culled at the end of their current parity (RR), as well as a beef females total expected number of parities (ENP) to complete, given her probability of surviving each parity. Parity 0 represents heifers.

Parity	PNext	Psurv	RR
0	1.000	1.000	0.838
1	0.773	1.000	0.806
2	0.812	0.773	0.752
3	0.828	0.628	0.689
4	0.825	0.520	0.624
5	0.812	0.429	0.553
6	0.796	0.349	0.478
7	0.774	0.278	0.398
8	0.742	0.215	0.304
9	0.707	0.159	0.183
10	0.660	0.113	0.183
ENP		5.464	

The total expected number of parities (ENP) that a beef female was estimated to complete if not culled (Eq. 7), given her probability of surviving each parity x ($Psurv_x$) is described in Table 5.3. For cows under consideration for culling that have already survived beyond the 9th parity limit, it was assumed that she had the same replacement requirements as if she were to be culled at the end of parity 9 (i.e., RR_9) with an expected maximum survival for only one additional parity. A beef female’s ENP was calculated as:

$$ENP = \sum_{x=0}^{10} Psurv_x \qquad [7]$$

where $Psurv_x$ is the probability of surviving beyond parity *x* so that the next parity (i.e., i*) is started and is calculated as:

$$Psurv_x = \begin{Bmatrix} 1, & when\, x = 0 \\ \prod_{j=1}^{x} Pnext_{j-1} & when\, 0 < x \leq 10 \end{Bmatrix} \quad [8]$$

where $Pnext_j$ is as described previously in Eq.6. It was assumed that all heifers chosen as replacements will start their first parity.

The cost of buying in a replacement heifer was captured in the term *Hrcost* and was estimated to be €1790 (Supplementary Table 9.7). The estimate of the salvage value of the cull cow in parity *x* ($f(Cullwt_x)$) was calculated from a function of average predicted cull cow carcass weight for an Irish beef cow (described later) completing parity *x* and combines intersecting linear and quadratic equations as follows:

$$f(Cullwt_x) = \begin{Bmatrix} a + b(Cullwt_x) + c(Cullwt_x^2) & if\, Cullwt_x < T \\ d(Cullwt_x), & otherwise \end{Bmatrix} \quad [9]$$

where *a* to *d* and *T* were estimated using the price data described in detail below; this shape is based on the pricing model adopted in Irish abattoirs. The predicted cull carcass weight ($Cullwt_x$) was calculated as:

$$Cullwt_x = PV_{cullwt} + LSMCullwt_x \quad [10]$$

where PV_{cullwt} is the production value for a beef female's cull cow carcass weight. Least squares means of the cull cow carcass weight for parity *x* ($LSMCullwt_x$) was estimated from an Irish dataset of 86,949 cull cows with a linear fixed effects model fitted to cull cow carcass weight adjusting for parity, carcass fat, conformation and EBV for cull cow weight (described in detail below); the *LSMCullwt* estimates for parity x are detailed in Supplementary Table S9.8.

5.3.2 Transition matrices

The probability of an animal transitioning from one state to another, over a period of time, was calculated using Markov transition matrices similar to the methodology described by Kelleher et al. (2015) for dairy cows.

1) Month of calving group fertility transition matrix

A three dimensional (i.e., a 9 × 11 × 5 matrix array) fertility transition matrix was constructed. The transition matrix dimensions were calculated as follows: firstly, animals were classified into 9 groups based on their most recent MOCG, namely: (1) January, (2) February, (3) March, (4) April, (5) May, (6) June, (7) July and August, (8) September, and (9) October to December, inclusive (Table 5.4); secondly, animals were partitioned into 12 transition states based on their MOCG in the next lactation and the duration of time between consecutive calvings as described in Table 5.4; finally, animals were stratified into 5 percentile groups of equal size based on their PV for CIV (i.e., $PG(PV_{CIV})$; Eq. 4). Solely for the construction of the transition matrices, and to avoid the potential of biasing the matrices with the animal's own records, PVs for the transition matrices were calculated using the female's parental average EBV for CIV plus their own heterosis effect on calving interval estimated from the national genetic evaluation where it exists as a fixed effect.

2) Survival transition matrix

A three dimensional (i.e., a 9 × 8 × 5 matrix array) survival transition matrix was constructed as follows: firstly, animals were classified into 9 groups based on their most recent MOCG (Table 5.4); secondly, animals were stratified based on their current parity number group as 1, 2, 3, 4, 5, 6, 7, 8 to 10, inclusive; finally, animals were stratified into 5 strata of equal size based on their survival PV (i.e., $PG(PV_{su})$ Eq. 4). The survival PV used within the survival transition matrix was calculated using the animal's parental average EBV for survival plus the beef female's own heterosis effect on survival estimated from the national genetic evaluation where it exists as a fixed effect.

Table 5.4: Month of calving groups (MOCG) defined to describe the current state and transition state beef female's month of calving groups as well as the time period between the consecutive calving used in the estimation of the calving interval and survival transition matrices.

MOCG	Current state	Transition state	Calendar years between successive calving
1	January	January	1
2	February	February	1
3	March	March	1
4	April	April	1
5	May	May	1
6	June	June	1
7	July and August	July and August	0 or 1
8	September	September	0 or 1
9	October to December	October to December	0 or 1
10	-	January	2
11	-	February and March	2
12	-	April to August	2

5.3.3 Data used in the construction of the index

Genetic and non-genetic effects, as well as the associated raw phenotypic data, were available from the Irish Cattle Breeding Federation (ICBF) national database, Bandon, Co. Cork, Ireland (http://www.icbf.com). The data used in the construction of the BFPP were calving records pertaining to the Irish national herd which were available on 3,850,256 beef females. Cows were classified as beef provided they had less than or equal to 50 % dairy breed composition (i.e., Friesian, Holstein and Jersey). To ensure the data analysed were representative of the Irish national commercial beef herd, animals were removed if they were registered to a breed society or were recorded to have given birth to a calf from embryo transfer; these edits resulted in 3,377,598 cows remaining. Only animals that calved between the years 2012 and 2017, inclusive, for parities 1 to 11, inclusive were retained. Erroneous data and calving events with calving intervals (i.e., the number of days between two consecutive calvings) that were below 300 d or exceeded 600 d were removed and if the calving interval was removed, the animal was recorded to have not survived; these edits resulted in 1,598,271 cows with 4,281,355 calving events remaining. When calculating the transition matrices, parental average

EBVs were used; therefore the beef female's sire and dam as well as their respective PTA for CIV and survival were required to be known; a total of 2,218,278 records from 786,487 cows remained. Herds were also required to have a minimum of 5 calving events each year which resulted in 1,789,373 records from 689,438 animals used in the development of the CP and FP components of the BFPP index.

Further edits were applied to the dataset for the estimation of the function values within Eq. 9 and the $LSMCullwt_x$ (Eq. 10) within the RV component. Animals were required to have cull cow carcass phenotypes including carcass weight, conformation and fat, as described in Englishby et al. (2016), as well as price per kg of carcass weight; 270,745 beef females remained. Animals were also required to have not gone through a fattening period, therefore if cows were harvested over 300 d from their last calving they were removed, resulting in 86,949 beef cows remaining. Using SAS 9.4 software (SAS Institute Inc., Cary, NC), the function values embedded within Eq. 9 were estimated using a linear and non-linear regression model in PROC NLIN. The carcass weight break-point (*T*) was calculated as: $-0.5\left(\frac{b}{c}\right)$; the upper limit euro / kg of carcass weight (*d*) was calculated as: $a + b(-0.5\left(\frac{b}{c}\right) + c\left(-0.5\left(\frac{b}{c}\right)\right)^2$.

5.3.4 Index validation

The validation population was based on all beef cows that had a recorded calving event in the year 2017 within the edited dataset; the following additional edits were applied: 1) beef cows were required to have EBVs for each trait within the Replacement index (RIndex) available, resulting in 150,370 cows, 2) beef cows were retained if their resulting progeny from the 2017 calving were harvested prior to data extract between 12 and 36 months of age for heifers and steers and between 12 and 24 months of age for young bulls; 124,992 beef females remained; 3) the sires of the beef cow's progeny were required to have been known and the progeny must have resided in the herd prior to slaughter for at least 100 days; 94,944 beef cows remained; 4) at least three animals must have been present in the progeny's slaughter contemporary group, resulting in 72,059 beef cows remaining and finally, 6) there had to be at least 15 calving events in the herd in 2017 for the beef females to be retained; this resulted in 21,102 beef cows from 875 herds remaining in the validation population as well as 21,102 of their harvested progeny.

5.3.5 Genetic evaluations

Five suites of multi-trait multi-breed genetic evaluations were run to generate both random and fixed effects solutions for all traits included in the Irish national replacement beef index using the Mix99 software (MiX99 Development Team, 2015). The phenotypic data pertaining to the five genetic evaluations were truncated on the 31/12/2017 and therefore only included records pertaining to the beef females for, and prior to, the year 2017. The national fertility evaluation is a 6 × 6 multi-trait evaluation. The fertility phenotypic data used in the present study consisted of 11,186,677 individual lactations with a pedigree file of 15,321,093 animals; fixed effect solutions and random effects pertaining to age at first calving (AFC; days), calving interval (CIV; days) and survival (surv; %) were retained. The national calving performance evaluation is a 9 × 9 multi-trait evaluation and included 19,555,773 birth records with 23,719,121 animals in the pedigree file; fixed effect solutions as well as random direct and maternal effects were available for the traits calving difficulty (scale 1 to 4), mortality and gestation length (days). The docility genetic evaluation is a 3 × 3 multi-trait genetic evaluation; the phenotypic data used in the present study consisted of 2,761,478 individual animals, with a pedigree file of 4,172,537 animals; fixed effect solutions and random effects pertaining to the farmer recorded calf and cow docility traits were retained. The national beef carcass evaluation is a 29 × 29 multi-trait carcass genetic evaluation; the phenotypic dataset consisted of 13,347,345 individual animal's records and the pedigree file contained 18,918,306 animals; fixed and random effect solutions pertaining to cow live-weight, feed intake, carcass traits (i.e., weight, conformation and fat) and, cull cow carcass weight were used in the present study. The national milk (i.e., maternal weaning weight) genetic evaluation is a 7 × 7 multi-trait evaluation; fixed effect solutions as well as maternal and direct random effects were retained for weaning weight; the phenotypic data used in the evaluation consisted of 8,802,215 individual animals and the pedigree file contained 13,428,159 animals.

5.3.6 Statistical analyses

Within each herd, Pearson correlations were used to estimate the relationship between the BFPP index itself, three of its sub-indexes (as there were no heifers in the validation population, the HP component was omitted from the validation), the Irish national maternal replacement (Rindex), the calf (comprised of terminal traits) and cow (comprised of maternal traits) sub-indexes of the Rindex, and the Irish national terminal index. The pairwise correlations were subsequently averaged across herds. Within each herd, animals were stratified into four groups of equal size based on their BFPP index value. A range of descriptive statistics were estimated for each stratum as well as the CP, FP and RV sub-indexes. The association between cow calving interval with each stratum was estimated by adjusting for contemporary group of calving. The log of the odds of surviving was estimated using logistic regression in PROC GENMOD (SAS Institute Inc., Cary, NC) as follows:

$$Logit\{P(Surv = 1|X)\} = BFPPStrata + HYScalv$$

where $Logit\{P(Surv = 1|X)\}$ was the log of the odds of a positive outcome (i.e., the animals survived); *BFPPstrata* represented the fixed effect of the beef cow's stratum for BFPP (i.e., 1 to 4, inclusive); *HYScalv* was the random effect of the cow's herd-year-season contemporary group of calving. Odds ratios were calculated as the exponent of the model estimate solutions.

Linear mixed models were used to estimate the least squares means of each stratum for the progeny traits as:

$$\begin{aligned} Carcass\ traits_a &= BFPPStrata + \sum_{b=1}^{2} Het + HYSslau + CarcType + AgeSlau \\ &+ SirePTA_a + CarcType|AgeSlau + CarcType|SirePTA_a + e \end{aligned}$$

$$\begin{aligned} AgeSlaughter &= BFPPStrata + \sum_{b=1}^{2} Het + HYScalv + CarcType \\ &+ CarcassWeight + CarcassFat + CarcType|CarcassWeight \\ &+ CarcType|CarcassFat + e \end{aligned}$$

where *Carcass traits* was the trait *a* pertaining to carcass weight (kg), conformation (EUROP scale) and fat (15 point score); *AgeSlaughter* was the age of the progeny when harvested (in days); *BFPPstrata* represented the fixed effect of the beef cow's stratum for BFPP (i.e., 1 to 4, inclusive); *Het* was the heterosis coefficient which is fitted as two separate fixed effect heterosis coefficients to represent the progeny of the beef cows different breed crosses; *HYSslau* and *HYScalv* were the progeny of the beef cows herd year season contemporary group for slaughter and birth, respectively, fitted as a random effect; *CarcType* was the fixed effect of whether the progeny was a heifer, steer or young bull; *AgeSlau* was the fixed effect of the progeny's phenotypic age at slaughter in months; *SirePTA* was the progeny's sire PTA for trait *a*, fitted as a fixed effect; *CarcType| AgeSlau* was the fixed effect interaction between the progeny's carcass type and age at slaughter; *CarcType|SirePTA* was the fixed effect interaction between the progeny's carcass type and sire's PTA for trait *a*; *CarcassWeight* was the fixed effect of phenotypic carcass weight (kg) of the progeny; *CarcassFat* was the phenotypic carcass fat score of the progeny, fitted as a fixed effect; *CarcType|CarcassWeight* was the fixed effect interaction between the progeny's carcass type and phenotypic carcass weight; *CarcType|CarcassFat* was the fixed effect interaction between the progeny's carcass type and phenotypic carcass fat; e is the residual.

5.4 Results

5.4.1 Characterisation of components within the BFPP index

Irrespective of parity or MOCG, the probability of surviving from one parity to the next progressively improved as the percentile group for survival PV improved, (Figure 5.1). The difference in survival between the best and worst PV percentile groups ranged from 9.65 % for third parity cows calving in February to 20.95 % for parity one cows calving in June. Cows that calved in either January or February tended to have the greatest probability of surviving to next parity across all PV percentile groups. Irrespective of PV percentile group or MOCG, parity 2 to 6 cows, inclusive, had a greater probability of survival to the next parity than parity one animals. The lowest probability of surviving to the next parity was for cows that calved in July and August (Figure 5.1); the survival transition matrix data are in Supplementary Table 9.9.

Cows that calved between January and April, inclusive, had a greater probability of re-calving in the same MOCG the following year (ranging from 0.29 in the lowest PV group for January to 0.45 in the best PV group for March) relative to transitioning into a different MOCG (Figure 5.2). Irrespective of the MOCG, the cows with the highest PV percentile group for CIV had a greater probability of re-calving in the same MOCG relative to the lowest PV percentile group. Cows in the best PV stratum for CIV also had a greater probability of re-calving earlier relative to cows in the worst CIV stratum; whereas cows in the lowest PV stratum for CIV had a greater probability of re-calving later relative to cows in the best PV stratum (Figure 5.2). The fertility transition matrix values are available in Supplementary Table S9.10.

Within the RV component of the BFPP index, the beef female's salvage value was determined by: 1) the constant value a equal to -3.309, 2) the linear coefficient of 0.037111 and, 3) the quadratic coefficient -0.0000506. Thus, the cull cow carcass weight break-point value (*T*) was estimated to be 366.71 kg (i.e., $T = -0.5\left(\frac{0.037111}{-0.0000506}\right)$). The upper limit Euro per kg of cull cow carcass weight, d, was estimated to be €3.50 per kg (i.e., $d = a + b(T) + c(T^2)$). Therefore, the formula used in the estimation of the beef females cull cow carcass value was:

$$f(Cullwt_x) = \begin{cases} -3.309 + 0.037111(Cullwt_x) + -0.0000506(Cullwt_x^2) & if\ Cullwt_x \\ 3.50(Cullwt_x), & otherwise \end{cases} \quad [11]$$

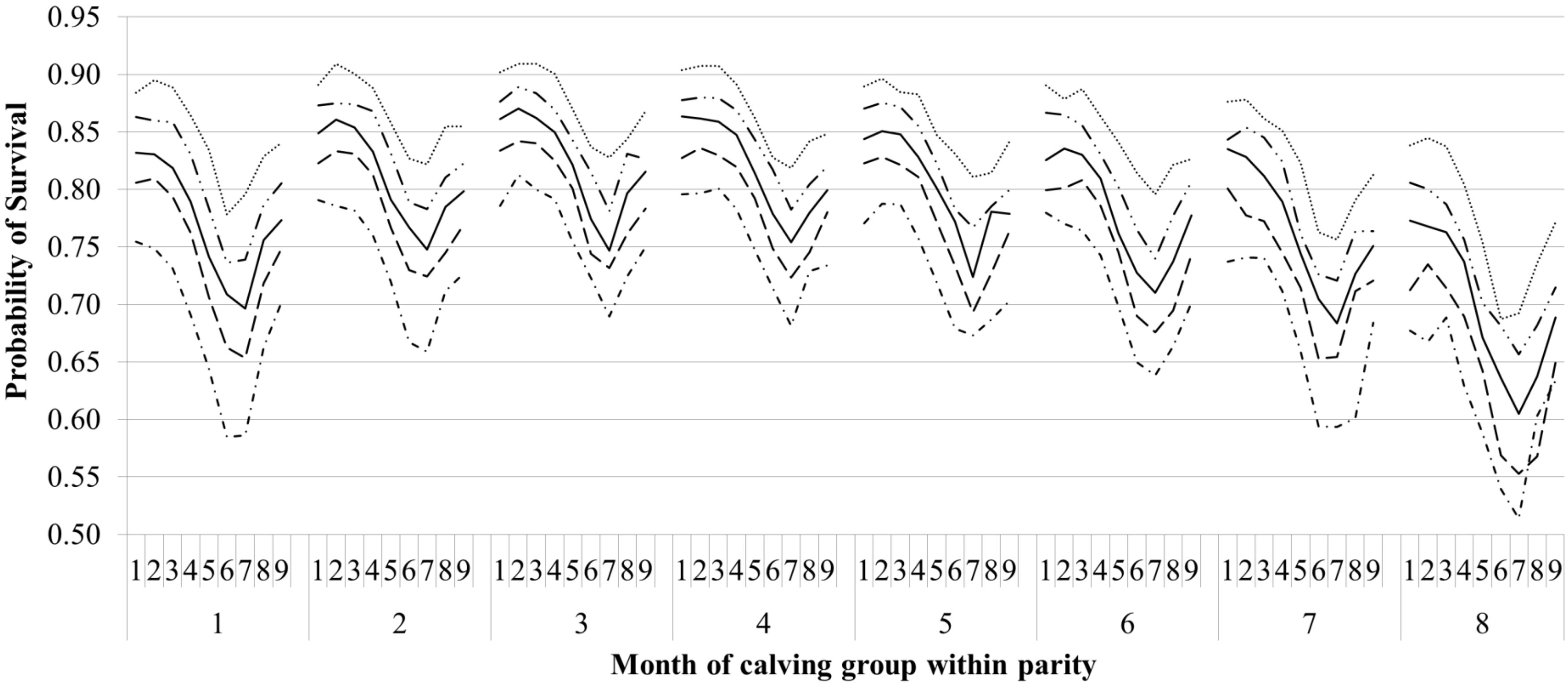

Figure 5.1: The probability of beef females, stratified into 5 strata based on their parental average estimated breeding value for survival (i.e., top 20% (••••), 60 % to 80 % (─ • •), 40 % to 60 % (──), 20 % to 40 % (── ──), and bottom 20 % (─ • ─)), surviving to start a subsequent parity given their current month of calving group (i.e., 1= January, 2 = February, 3 = March, 4 = April, 5 =May, 6= June, 7 = July and August, 8 = September and 9 = October to December, inclusive).

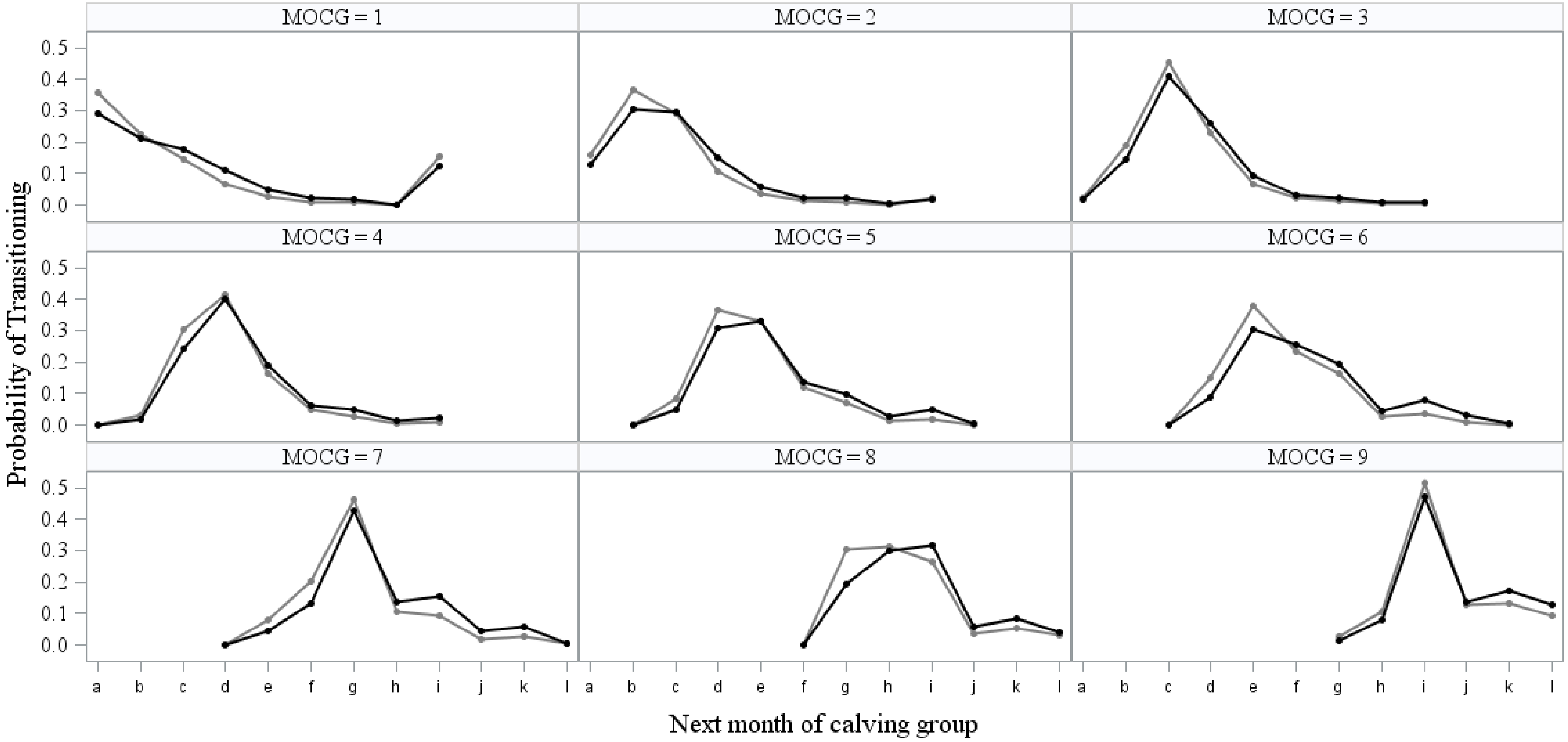

Figure 5.2: The probability of beef females within the top (grey) and bottom (black) 20% strata for their parental average estimated breeding value for calving interval and heterosis effect transitioning to a next month of calving group (i.e., a = January, b = February, c = March, d = April, e =May, f = June, g = July and August, h = September, i = October to December, j = January, k = February and l = April to August, inclusive, where groups j to l are in two calendar years' time), given their current month of calving group (MOCG; i.e., 1= January, 2 = February, 3 = March, 4 = April, 5 = May, 6= June, 7 = July and August, 8 = September and 9 = October to December, inclusive).

5.4.2 Descriptive summary of the BFPP index

The correlations between all the (sub-) indexes are in Table 5.5. Of the three sub-indexes in the BFPP, the FP was the most strongly correlated with BFPP (r = 0.84) whereas the RV was the most weakly correlated (r=0.49). The BFPP was moderately positively correlated with the Irish national replacement index within herd (i.e., Rindex; r = 0.45) as well as with both the calf (r = 0.29) and cow (r = 0.31) sub-indexes of the Rindex. The correlation between the BFPP and the Irish national beef terminal index was much weaker at 0.27. Of the three sub-indexes of the BFPP, the FP sub-index was most strongly correlated with the Rindex (0.63) with correlations of 0.40 and 0.47 with the cow and calf sub-indexes of the Rindex, respectively. Although the correlation between the CP sub-index and the Rindex was only 0.17, the correlation between the CP and the calf sub-index (r = 0.28) was stronger than the correlation of 0.03 between the CP and the cow sub-index. While the correlations reported above are for 875 herds with at least 15 calving’s, the correlations were very similar when the dataset was limited to the 256 herds with at least 25 calving’s.

Table 5.5: Correlations between the Beef Female’s Profit Potential index (BFPP) and the current parity (CP), future parity (FP), retention value (RV) components within the BFPP index, as well as the Irish national Replacement index (Rindex), the calf (Calf Rindex) and cow (Cow Rindex) sub-indexes within the Rindex and the Irish national Terminal index.

	CP	FP	RV	Rindex	Calf Rindex	Cow Rindex	Terminal
BFPP	0.68	0.84	0.49	0.45	0.29	0.31	0.27
CP		0.55	-0.07	0.17	0.28	0.03	0.29
FP			0.14	0.63	0.47	0.40	0.45
RV				0.06	-0.15	0.14	-0.16
Rindex					0.29	0.86	0.22
Calf Rindex						-0.18	0.98
Cow Rindex							-0.24

5.5 Validation of the BFPP index

The average within-herd BFPP index and BFPP sub-index values by quartiles are in Figure 5.3. As BFPP stratum improved, the mean BFPP index and sub-index values also increased. The smallest mean difference between the best and worst strata was within the RV sub-index (i.e., €121.64), whereas the greatest difference was within the FP sub-index (i.e., €246.92). Cows within the top 25 % BFPP stratum had the largest range of (sub-) index values relative to the remaining strata (Figure 5.3). The mean Irish national replacement index (breeding index for maternal beef traits; Rindex) and Terminal index (breeding index for terminal beef traits) for each BFPP stratum is in Table 5.6. As the BFPP stratum improved, the Rindex and terminal index values also improved. The mean Rindex of cows in the best BFPP stratum was €35.73, therefore the additional profit expected from each of the cow's calving's was expected to be worth €35.73 more than cow's within the worst stratum. The mean terminal index value of the cows within the best stratum was almost €16, thus the harvested progeny of the high BFPP beef cows were, on average, expected to be almost €16 more profitable than the progeny of the beef cows within the worst BFPP stratum.

The mean phenotypic performance of both the beef cows and their progeny for each within-herd BFPP stratum are also in Table 5.6. Cows within the top 25 % for the BFPP had the longest calving interval, 8 days, on average, longer than the bottom 25% of cows on BFPP. The top 25 % BFPP ranked cows, however, were 1.63 times more likely to survive to the next lactation than the lowest ranking contemporaries. When the progeny of the high BFPP cows were harvested, they had, on average, heavier more conformed carcasses with lower fat scores relative to the worst BFPP stratum. When adjusted to the same carcass weight, the progeny of the high BFPP cows were, however, harvested almost 8 days later than the progeny of the beef cows within the worst BFPP stratum (Table 5.6).

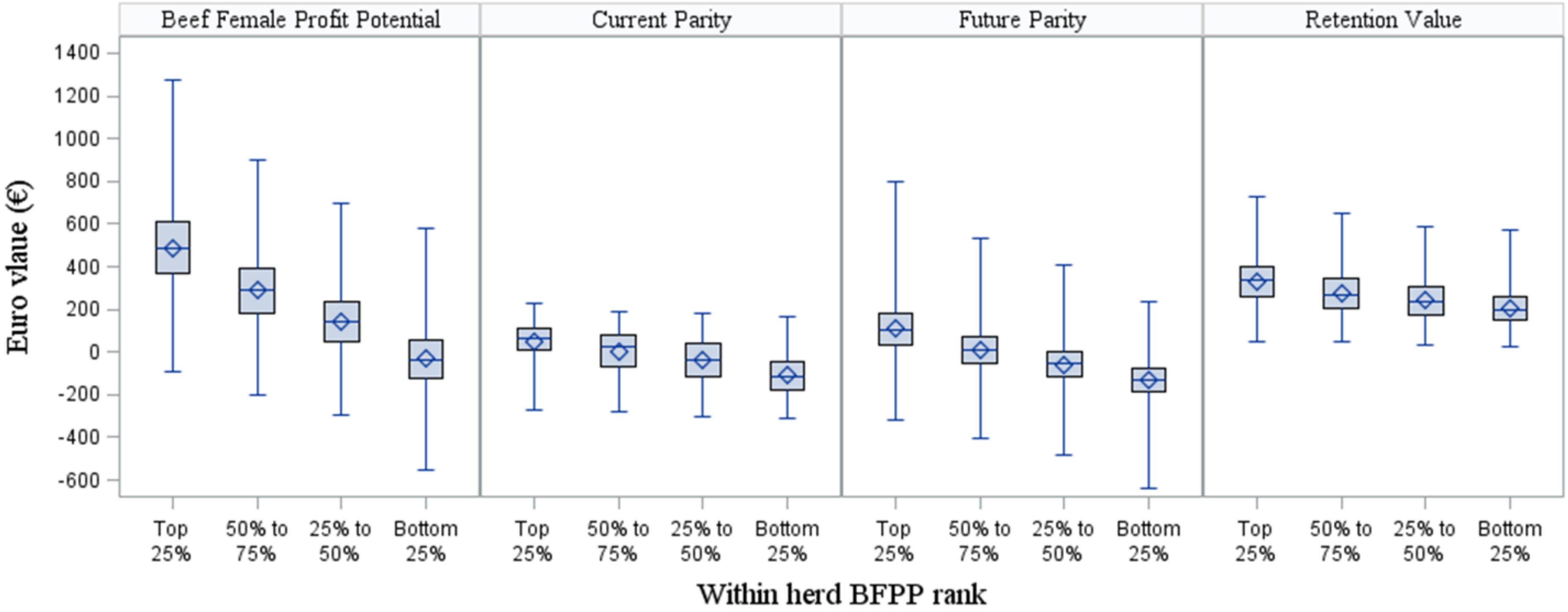

Figure 5.3: Summary statistics of the Beef female profit potential (BFPP) index as well as the individual component used to calculate the BFPP, including the current parity, future parity and retention value components within the four strata based on the within herd ranking of animals using the BFPP index.

Table 5.6: Mean Irish national Replacement and Terminal index values for animals stratified based on their Beef Female's Profit Potential (BFPP) index value, as well as the least square means performance of BFPP female's progeny for carcass traits (i.e., weight, conformation and fat) and age at slaughter; standard error within parenthesis.

		Beef Female Profit Potential stratum			
Animal	Component	Top 25%	50% to 75%	25% to 50%	Bottom 25%
Cows traits	Replacement (€)	32.76 (30.05)	22.35 (30.16)	12.75 (30.73)	-2.93 (32.60)
	Terminal (€)	31.97 (28.45)	27.61 (28.26)	23.27 (28.97)	16.07 (29.96)
	CIV (days)	377.21 (39.03)^{a}	372.33 (39.32)^{b}	371.26 (39.71)^{b}	368.87 (40.98)^{c}
	Survival[1] (0 to 1)	1.63 (1.52,1.73)^{a}	1.48 (1.39,1.58)^{a}	1.34 (1.25,1.43)^{a}	1.00 (1.00,1.00)^{b}
Progeny traits	Carcass weight (kg)[2]	398.46 (59.76)^{a}	398.48 (59.76)^{a}	396.61 (59.76)^{ab}	394.29 (59.76)^{b}
	Carcass Conformation (EUROP scale)[3]	7.19 (1.74)^{a}	7.14 (1.74)^{ab}	7.07 (1.74)^{b}	6.94 (1.74)^{c}
	Carcass fat (1 to 15 scale)[4]	7.94 (1.65)^{a}	7.99 (1.65)^{ab}	8.04 (1.65)^{b}	8.04 (1.65)^{b}
	Age at slaughter (days)[5]	659.28 (129.28)^{a}	653.90 (129.28)^{b}	652.42 (129.28)^{b}	650.45 (129.28)^{b}

Different superscripts within row indicate significance difference $P < 0.05$

[1] The bottom 25 % BFPP stratum was the reference stratum.

[2] Reference animal was a steer with 100% heterosis, slaughtered at 24 months old and sires carcass weight PTA was 20kg.

[3] Reference animal was a steer with 100% heterosis, slaughtered at 24 months old and sires carcass conformation PTA score was 1.6 units.

[4] Reference animal was a steer with 100% heterosis, slaughtered at 24 months old and sires carcass fat PTA score was -0.06.

[5] Reference animal was a steer with 100% heterosis, slaughtered at 24 months old with a carcass weight of 380 kg and carcass fat score of 6.8.

5.6 Discussion

Culling decisions have been reported to be multifarious (Bascom and Young, 1998) and can be influenced by a range of factors such as age (Adamczyk et al., 2017), performance relative to contemporaries (Berry et al., 2005), infertility and production (Seegers et al., 1998). Hence, actually deciding on which animal to cull given all the underlying contributing factors can become unwieldy, especially in large herds. A fundamental element to the successful deployment and adoption of any decision-support tool (DST), such as the BFPP, is providing an actual solution to a problem. Therefore, being able to collate the multifarious risk factors into a single rank per animal could be hugely beneficial in achieving more optimal culling decisions. Several tools have previously been developed to help identify animals for culling (Stewart et al., 1977; Lopez-Villalobos et al., 2010), yet to our knowledge, all are specific to the dairy sector. To date, the quality and availability of data pertaining to genetic-based beef management DST may have been a limiting factor in the ability to develop and implement a culling tool, such as the BFPP; therefore the international applicability of the BFPP framework may be data resource-limited and would require data integrity systems in place which ensure sire verification.

Key drivers of the successful adoption and on-going engagement with a DST are multitudinous and include factors such as the DSTs ease-of-use, potential to improve efficiency as well as the trustworthiness of the provider (Rose et al., 2016). Hence, incorporating components within the DSTs which are already familiar and trusted by the producer (e.g., breeding indexes) can stimulate an accelerated rate of adoption. Furthermore, being able to demonstrate the construction of the final index value by decomposing it into its individual sub-components can facilitate a greater understanding, and thus acceptance, of the ranking tool. This was the basis of the approach adopted by Kelleher et al. (2015) in their construction of a relatively simply tool to rank dairy cows on future lifetime profitability. The motivation for the present study was to tailor, and where appropriate, modify the framework proposed by Kelleher et al. (2015) for deployment in beef females; a noteworthy addition in the present study to the tool proposed by Kelleher et al. (2015) was its expansion to also consider nulliparous females in the ranking against cows. This important addition can be beneficial in deciding whether a virgin heifer should be retained as a replacement or finished for harvesting.

Similarly, the ability to compare the BFPP of a virgin heifer to that of the cows in the herd can help determine the level of voluntary culling for that herd. The end outcome is that the BFPP proposed within should be used to first and foremost identify cows for culling (and the heifers to replace them), but can also be used to identify superior females with the greatest lifetime potential within the herd. When utilised in tandem with a maternal breeding index (Twomey et al., 2020), females who are not only genetically superior, but also have a high BFPP value, and therefore a high lifetime profitability potential, can be identified and mated to suitable bulls to produce exceptional replacement females and in doing so, increase the genetic gain achievable; the end outcome being a year-on-year improvement in performance. The BFPP can also facilitate the decision-making process when trading beef females as the buyer can assess the future lifetime potential of the female. Moreover, although the research was carried out on dairy cattle, Dunne et al. (2019) reported that an animal's performance can differ depending on the herd's best linear unbiased estimates; therefore, there is potential for the BFPP to be tailored to each individual herd so that producers have an indication of how a female may perform specific to their own herd environment.

5.6.1 Framework of the culling tool

Selection indexes were first proposed in the early 1940's (Hazel and Lush, 1942) and are now ubiquitous in animal breeding globally. Ireland operates both a terminal (Connolly et al., 2016) and maternal (Amer et al., 2001; Twomey et al., 2020) national breeding index, both of which are routinely used by producers and breeders. The Irish maternal index forms the foundations of the proposed BFPP in the present study. Inclusion of both non-additive genetic effects and non-genetic effects is a key extension for implementation of this DST. The contribution of non-additive genetic effects (Gregory et al., 1978; McHugh et al., 2019) as well as non-genetic effects (Coyne et al., 2019; Judge et al., 2019; McHugh et al., 2019) to animal performance in beef cattle has been documented elsewhere; hence, these factors will influence the decision to cull a female (as well as which heifer to retain for breeding) and thus should be considered within a decision support tool for culling and identifying profitable heifers.

The underlying principle of the BFPP was that of the simple culling index developed for dairy cows by Kelleher et al. (2015) but modified to be applicable for beef females. Consistent with the BFPP developed in the present study, Kelleher et al. (2015)

considered the sub-indexes of the current lactation (CP in the present study), future lactations (FP in the present study) and what they called net replacement cost differential (RV in the present study). While most dairy breed females born are destined to become replacements (Kelleher et al., 2016), this is not necessarily the case in most beef enterprises with a proportion of females being grown for harvesting at, on average, 21 months of age (Berry et al., 2020). A decision therefore needs to be made relatively early in the life of the heifer, as to whether she is suitable to become a cow or would she be more profitable if harvested directly. To facilitate this decision point, the BFPP was expanded beyond that of the dairy index proposed by Kelleher et al. (2015) to also consider nulliparae. The end-purpose of the beef female is generally decided upon after weaning (approximately 8 months of age in Ireland; McHugh et al. 2014). Given that McHugh et al. (2014) also reported that the average AFC for a beef female was approximately 31 months, a time delay of almost 2 years between deciding to keep the female as a replacement and her calving for the first time would be expected to lapse. To reflect this time-delay, the HP sub-index of the BFPP was developed to be adaptable to specific decision-time points, with the addition of y (i.e., the estimated number of years until a heifer is predicted to express the trait under consideration), thus ensuring that producers are provided with BFPP index values that are representative of their nulliparous females at important time-points when decisions are being made.

The transition matrices developed in the present study are instrumental in modelling the lifetime efficiency potential of the beef female and are intrinsic to the FP sub-index. The fertility transition matrix was formulated to ultimately estimate the expected profit resulting from the beef female's next parity given her probability of calving in each MOCG. In a cross-sectional analysis of the Irish national database, McHugh et al. (2014) demonstrated how 38,619 Irish cows excelling in genetic merit for calving interval had shorter calving intervals. This observation corroborates the results from the fertility transition matrices in the present study (Figure 5.2 and Supplementary Table S9.10) where cows of superior genetic merit for calving interval had the highest probability of re-calving in the same or earlier MOCG relative to the contemporaries of poorer genetic merit for calving interval. This is despite the low heritability estimated for calving interval in the Irish beef cow population ($h^2 = 0.02$; Berry and Evans, 2014). Cows within the best BPFF stratum did, however, have an average phenotypic calving interval of 8 days longer than the cows within the worst BFPP stratum, even though their mean PV for CIV only differed by 0.78 of a day. Given that the genetic standard deviation for CIV from the genetic evaluation was estimated to be 5.43 days, very little difference existed in the genetic merit for CIV between the strata.

Animal survival can have a huge impact on herd profit since not only are calves from older cows more valuable (McHugh et al., 2010), owing to their superior carcass weight (Judge et al., 2019) but also because of the reduced requirement for replacement heifers who, in turn, can then be harvested. In their analysis of 5,582 Irish beef cows from the national database, McHugh et al. (2014) reported that the logit of the probability of survival to next lactation increased linearly as PTA for survival improved again consistent with the results from the survival transition matrices in the present study; the heritability of survival in Irish beef cows is 0.02 (Berry and Evans, 2014). Cows in the top stratum for PV for survival in the present study had between a 9.65 to 20.95 percentage unit greater probability of surviving to next lactation across the different MOCG, relative to the lowest PV stratum. A similar trend was corroborated in the validation whereby the odds of animals within the best BFPP stratum surviving was 1.63 times more likely than the worst stratum. Nevertheless, as Irish beef production is predominantly a spring-calving based system (Berry and Evans, 2014), animals had the highest probability of surviving if they calved within the first three months of the year, regardless of their PV stratum for survival.

One of the main objectives of the present study was to develop a tool that can easily be used by producers since this is a key criteria for successful adoption (Rose et al., 2016). This ease-of-use means that all the traits and underlying data are collapsed into a single value (i.e., the BFPP is provided from which to rank animals) and the data which populates the index is generally readily available and thus the marginal cost of generating the index is low. Most of the data underlying the developed BFPP in the form of fixed and random effects solutions are already routinely generated from genetic evaluations; therefore, the solutions should be relatively easy to obtain. Moreover, the potential users of the proposed BFPP are more than likely already engaging with the maternal breeding index and, therefore trust the information generated from the genetic evaluations; having this trust in a DST is a key factor potential users consider when deciding whether or not to adopt a new DST (Rose et al., 2016). Other components driving the BFPP of an animal such as the transition matrices or the cull cow prices do not need to be regularly updated. Of course, the index itself can be modified to, for example, incorporate a dynamism for costs and prices reflective of the seasonal variability. Notwithstanding this, the objective of the present study was to develop the framework and any such modifications would be easy to implement in the future.

5.6.2 Breeding versus management indexes and their applications

The BFPP is not designed to replace a maternal breeding index but instead to be complementary to such a breeding tool. The goal of most cow-calf producers is to shift the herd distribution of profit per cow in the favourable direction. A shift in the distribution can be achieved by breeding the females on the favourable side with genetically elite sires or by culling the females on the unfavourable side of the distribution. Fastest gain, of course, is achieved when both are applied together. In fact, the within herd correlation between the BFPP and the Irish national maternal index was 0.47 (Table 5.5) indicating that while both indexes are profit based, animals do indeed rank differently, albeit there is some similarities. This less than unity correlation is expected, partly because the breeding index trait predictions only includes additive genetic effects whereas the BFPP trait prediction also includes non-additive effects. Furthermore, the relative weightings on trait predictions is changed, and additional phenotypic attributes of the beef female are taken into consideration, such as her age, and most recent or expected month of calving . While a breeding index is generally used just prior to the start of the breeding season, the BFPP can be used at several points in the calendar year. Furthermore, breeding indexes are generally updated only a few times per year, synchronised with the relevant genetic evaluations. The BFPP, on the other hand, is developed to be dynamic and thus can be updated on the fly as new phenotypic information becomes available. This dynamic nature of the BFPP ensures that it is useful at multiple decision points during the calendar year.

Firstly a decision can be made, using the BFPP as to whether a cow should be mated that breeding season, or just culled. When deciding what females to breed replacements from, using the BFPP in conjunction with a breeding index ensures females with not only the greatest lifetime profit potential but, also the highest maternal genetic merit can be identified; thus shifting the distribution even further in a favourable direction. When the BFPP was validated, the complementary nature of both the BFPP and the maternal replacement indexes was reflected in the cow’s mean replacement index value. On average, the additional profit accruing from each cow's calving within the best BFPP stratum was expected to be worth almost €36 greater than the cows within the worst stratum; this was considered her genetic expectation. It was possible to estimate the actual monetary value arising from the differences in phenotypic performance between the best and worst BFPP stratum by multiplying the differences in performance (Table 5.6) by the respective economic value (Table 5.1). The difference in phenotypic performance of the cows in the best BFPP stratum relative to the worst, for survival and CIV was estimated to be worth an additional €10.20 and the phenotypic performance of their harvested progeny for the three carcass traits (weight, conformation and fat) was estimated to be worth an extra €21.92. Therefore, although not all traits were considered, it was estimated that the cows within the best BFPP stratum, on average, contributed an additional €32.31 per calving to the herd's profitability than cows within the worst stratum. Furthermore, the harvested progeny of the cows within the best BFPP stratum had a genetic expectation of being worth almost €16 more than the progeny of the worst BFPP cows, which is very close to the phenotypic difference of €21.92 estimated.

The dynamic nature of the BFPP means that when the cow calves, the most recent calving date can be used to update both the profit from the CP but also the likelihood of calving in different months of the following year (including not calving again) and thus the FP and overall BFPP. Following the breeding season, the BFPP can also be used once pregnancy diagnoses are recorded which generally occurs in the autumn time; if the cow is deemed not to be pregnant then she will not be calving the following calving season and should incur a large monetary penalty within the BFPP, similar to the dry cow penalty already incorporated. The decision can then be made to sell the cow for fattening or fatten the cow prior to slaughtering. Although both dairy and beef cows were included, McHugh et al. (2010) documented a bimodal distribution of when Irish cows were sold in livestock auctions, which were reported to coincide with prior to and post the breeding season; thus, there is huge potential for the BFPP index to provide data-driven culling decision-support during these times.

Once the subsequent calf is born, then the BFPP of the female calves can be used to identify the females most suitable for retention. Little additional information will become available on a nulliparae post birth other than through changes in her EBV either from genotyping or through changes in the EBV of her parents. One of the advantages of the reliance of the BFPP on data is that producers who want to optimally use the BFPP to their advantage must ensure the integrity and completeness of the data. These data can subsequently be used in the genetic evaluations to improve their accuracy of not only the female herself but her relatives and contemporaries. This in turn improves the accuracy of the BFPP, but also of the maternal breeding index. Therefore, the objectives of both indexes, while different, are very complementary.

5.7 Conclusions

Voluntary culling decisions are multifactorial and can be difficult to address, therefore the ability to collate the risk factors into a single BFPP value per animal could be hugely beneficial for users when making necessary culling decisions. The BFPP has the potential to be implemented complementary to a maternal breeding index and when used in combination, has the potential to add substantial value to the breeding index by facilitating decisions based on heifer replacements as well as cow culling decisions. Cows that ranked highly on the BFPP index had greater odds of survival, were more likely to calve in the same month the following year and produced calves of superior carcass metrics. The framework is ready for deployment in Ireland, but could also be considered for other industries where there is a reasonable level of sire verification and commercial cow and calf performance records captured in a central database system which are subsequently used in genetic evaluations.

Chapter 6:

Thesis Summary, Conclusions and Implications

6.1 Thesis Summary

The overall objective of the thesis was to explore opportunities of making better use of already existing data for both dairy and beef producers; the approaches and pipelines developed could, however, be applicable to other species (e.g., sheep). The thesis objective was achieved by: 1) investigating the potential information contained within best linear unbiased estimates (BLUEs) and the characterisation of such (Chapter 2), 2) quantifying the response to selection for additive and non-additive genetic merit by herd-level BLUE (Chapter 3), 3) developing a framework for a decision-support tool to rank growing cattle based on their genetic and non-genetic effects for carcass revenue to aid in more informed purchasing decisions (Chapter 4), and 4) developing an economic-based index to estimate a beef female's expected remaining lifetime productivity, thus facilitating the ranking and identification of females that should be retained or culled within the herd (Chapter 5).

All data used in this thesis originated from the ICBF national database; this included raw phenotypic data but also the outputs (i.e., BLUPs and BLUEs) from the national genetic evaluations operated by the ICBF as well as the associated pedigree data. All genetic evaluations were undertaken using linear mixed models in the MiX99 software suite (MiX99 Development Team, 2015). Multiple genetic evaluations were undertaken and the suites of traits included were: 1) dairy cow fertility (i.e., age at first calving (AFC), milk production, calving interval (CIV), calving to first service (CFS), number of services (NS) and survival (SU)), 2) beef calving (i.e., calving difficulty, mortality and gestation length), 3) beef cow milk yield (i.e., direct and maternal effects for weaning weight), 4) beef cow fertility (i.e., direct and maternal effects for AFC, CIV and SU), 5) beef docility (i.e., docility score) and, 6) beef carcass (i.e., carcass weight, carcass conformation and carcass fat), feed intake, cow live-weight and cull cow weight).

6.1.1 Chapter 1: Introduction and Review of the Literature

Objective: Review the existing literature pertaining to decision-support systems and tools, how they are applied in agriculture, and the decision-support tools that are currently available in the Irish cattle sector.

- Decision-support tools (DSTs) and systems (DSSs) are defined as software-based technologies that facilitate the decision-making process (Matthews et al., 2008; Rose et al., 2016) by means of interpreting data, applying the necessary analyses, and identifying evidence-based solutions (Dicks et al., 2014).
- The majority of animal breeding DSTs available worldwide have maximised genetic gain by applying statistical methods such as BLUP methodology developed by Henderson et al. (1959) and selection index theory developed by Hazel and Lush (1942).
- Irish animal-based DSTs were mostly breeding-based DSTs until 2017 when the Cow's Own Worth was launched for dairy females.
- Gaps in Knowledge:
    - Few studies have recognised the benefits of utilising BLUEs in herd management. To our knowledge, no study has quantified the response to selection of additive and non-additive genetic merit across a trajectory of herd BLUEs.
    - There is a void in management DSTs in the cattle sector to aid the transaction of growing animals destined for slaughter.
    - A DST that aids in the identification of females for culling purposes by ranking them based on their expected remaining lifetime profit is currently only available to dairy producers; no such DST exists for the beef sector.

6.1.2 Chapter 2: Characterisation of best linear unbiased estimates generated from national genetic evaluations of reproductive performance, survival, and milk yield in dairy cows

Objective: Describe herd-level factors associated with dairy herd-year BLUEs and understand the inter-relationship among herd-year BLUEs for milk, fertility, and survival traits.

- Raw phenotypes and herd BLUEs were available for: 1) age at first calving, 2) calving to first service (CFS), 3) calving interval (CIV), 4) number of services, 5) milk production and, 6) survival.
- The explanatory herd-level factors considered were: 1) geographical location, 2) whether or not the herd was milk recording, 3) herd size, 4) herd expansion rate, 5) herd-level use of AI, 6) the proportion of animals in the herd that calved within the first 42 days of the breeding season, 7) the proportion of animals that were registered to a breed society, and 8) the proportion of home-born and therefore not purchased in.
- Information was available on 88,730 herd-years from 8,873 herds over a 10-year period.
- Multiple regression linear mixed models were used to quantify the association between each herd-level characteristic (independent variable) and herd-year BLUEs for the 6 different traits (dependent variable).
- BLUEs were associated with two-thirds of the improvement in CIV and milk production in the 10 years prior to the study. Milk recording herds, on average, calved heifers 15 days younger than non-milk recording herds.
- Larger herds had, on average, worse BLUEs for both CIV and CFS. Expanding herds, on average, calved heifers younger and had the largest proportion of home-born animals.
- Results can be used to identify inferior herd management which may be compensated by superior genetics and *vice versa*; thus, BLUEs have a role in bespoke decision support.

6.1.3 Chapter 3: How herd best linear unbiased estimates affect the progress achievable from gains in additive and non-additive genetic merit

Objective: Investigate the existence of G × E interactions for fertility, production and survival traits across herds differing in BLUEs

- A subset of the data from Chapter 1 were used; the data originated from 1,764 herds with data for age at first calving (AFC) on 124,352 animals and data for milk yield, calving interval, number of services, calving to first service and survival on 216,270 animals.
- Genetic and residual (co)variances were estimated for each trait within 3 BLUE environments. Multiple linear regression mixed models were used to regress each trait's phenotypic value on its respective additive and non-additive genetic merit and how this interacted with herd BLUE.
- Within trait genetic correlations between the three BLUE environments were all stronger than 0.61 (except for AFC) suggesting no need for separate breeding programs.
- Genetic and residual SD tended to be largest in the best BLUE stratum for production traits whereas, for the remaining fertility and survival traits, the genetic and residual SD tended to be largest within the worst BLUE stratum.
- The response in phenotypic milk yield per kg increase in milk EBV in the best BLUE stratum was 20% greater than in the worst milk BLUE; the regression coefficient of phenotypic calving interval (CIV) on CIV EBV was 4.28 times larger in the worst BLUE environment relative to the best BLUE.
- Genetic evaluations assume a 1-unit change in EBV equates to a 1-unit phenotypic change, yet results from this study suggest that the response to selection differs by herd BLUE; therefore, the integration of herd-level BLUEs in a DST may contribute to more informed breeding decisions.

6.1.4 Chapter 4: Formulation of a decision support tool incorporating both genetic and non-genetic effects to rank young growing cattle on expected market value

Objective: Develop a framework for two decision support indexes capable of predicting the relative lifetime revenue of an animal for harvest taking cognisance of both additive and non-additive genetic effects as well as contributing non-genetic effects.

- The constructed Harvest index, which comprised of carcass weight, conformation and fat, was aimed at purchasers of animals close to harvest; the constructed Calf index, also included docility and feed intake and was aimed at purchasers of young calves for growing. All traits were weighted by their respective economic weight.
- The constructed indexes were calculated using three alternative estimates of an animal’s total merit: firstly, based solely on the animal’s breed solutions; secondly, based on the animal’s EBVs; and finally, based on the animal’s additive plus non-additive genetic effects, as well as its non-genetic contributing effects (production values [PV]).
- Indexes were validated on 874 bulls and steers with feed intake, carcass and live-weight phenotypes.
- Correlations between carcass revenue and both the Harvest and Calf index doubled in strength when the index was estimated using PVs relative to just the breed effects (i.e., from 0.22 to 0.44 and 0.20 to 0.40, respectively).
- Predictive ability of the indexes strengthened as live-weight phenotypes were incorporated within the indexes.
- Results from the present study suggest that greater predictive ability relative to carcass revenue can be achieved through the development of bespoke DSTs targeted towards cattle of all ages provided they will not become parents.

6.1.5 Chapter 5: An index framework founded on the future profit potential of beef female cattle to aid the identification of candidates for culling

Objective: Formulate the framework for a decision support tool that ranks beef females based on their expected remaining lifetime production potential, derived from their additive and non-additive genetics effects as well as environmental factors.

- The Beef Female's profit potential (BFPP) comprised of four sub-indexes including: 1) the animal's heifer potential (HP) until she first calves, 2) the remaining profit potential of the cow's current parity (CP), provided she has calved at least once, 3) the profit potential of the cow's future parities (FP) and finally, 4) the retention value (RV) of the beef female if she was to be retained within the herd.
- Each sub-index was estimated using production values (PVs) which comprised of genetic and non-genetic effects, thus capturing the beef female's total merit for a given trait.
- The female's future fertility and longevity potential was modelled using transition matrices.
- The BFPP was validated using 21,102 beef cows as well as 21,102 of their progeny.
- Beef cows were ranked, within herd, into four strata based on their BFPP value. Despite the beef cows in the best stratum having an average CIV almost 8 days longer than animals within the worst stratum, they had a 1.61 times greater odds of surviving and starting their next parity.
- The harvested progeny of the high BFPP cows had, on average, heavier more conformed carcasses with fat scores relative to their poor BFPP contemporaries.
- The cows identified for voluntary culling using the BFPP contributed, on average, €32 less per calving to the herd's profitability relative to the highest ranked females; therefore, it can be deduced that the BFPP can be used to identify inferior females for culling.

6.2 Thesis Conclusions and Implications

This thesis has identified, developed and demonstrated novel frameworks that aim to fill the voids that currently exist within both the dairy and beef animal-based DST repertoire. Results from the thesis described the various herd-level factors associated with BLUEs (Chapter 2) as well as revealed the additional value that can be acquired through the integration of such BLUEs in a DST (Chapter 3). Furthermore, the thesis also filled a void in the demand by the Irish cattle industry for a DST which better informs the value of both growing cattle (Chapter 4) and beef females (Chapter 5). Therefore, the implications of the thesis are: 1) identified uses of data and information for DSTs which heretofore have often been disregarded, 2) developed the background framework for DSTs to inform the transaction of growing cattle which are more accurate and dynamic than the tools and information (e.g., breed composition) available heretofore and, 3) formulated a framework to rank beef females based on their predicted remaining lifetime performance, similar to what was developed by Kelleher et al. (2015) for dairy females; this dairy-based DTS was deployed by the ICBF in 2017 and has a usership of approximately 30 % of the eligible national dairy herd (i.e., milk recording herds that are at least 80% spring calving) thus signifying the demand which may also exist in the beef industry. The DST proposed in Chapter 4 has already sparked interest from ICBF, the national body responsible for generating national genetic evaluations, and the index is currently being integrated into the ICT infrastructure at ICBF for future deployment; as two variants of a transaction index were developed in Chapter 4, the Calf and Harvest index, from hereon in both indexes will be generally referred to as a transaction index.

6.2.1.1 Decision support throughout the production cycle

Currently in Ireland the cattle genetic-based DSTs are either: 1) primarily focused on breeding and identifying genetically superior parents for future generations (assuming the animals will be managed in the average environment) e.g., EBI, DBI, Replacement and Terminal index or, 2) completely void in some sectors, i.e., the lack of a beef female C.O.W. DST. Whereas the DSTs proposed in this thesis have the potential to be deployed and not only fill the existing voids in decision support, but also act as complementary DSTs alongside the DSTs that are currently available. This is especially important given that when problems arise on-farm they tend to be interrelated (Rossi et al., 2014) and, if not doing so already, can have ramifications on production efficiency later on in the system. By applying the DSTs proposed in this thesis, the dairy sector will not only become more integrated with the beef sector (Chapter 4) but the Irish beef producer will also be provided with support throughout the whole production cycle (Chapter 4 and 5). The potential applications of BLUEs and the proposed DSTs developed within this thesis are illustrated in Figure 6.1. By defining the stages of the production cycle, it is possible to identify the key time points in the production cycle where BLUEs and the developed DSTs could be applicable. The chosen decision time points within the production cycle were: 1) *prior to mating,* 2) *BLUPs versus BLUEs*, 3) *Breeding,* and finally, 4) *Birth of calf*; indicated by the dark blue boxes in Figure 6.1.

6.2.1.2 Decision support time-point: prior to mating

The decision on whether or not to breed or cull a dairy or beef female in Ireland is generally undertaken either prior to the breeding season or close to drying off after pregnancy diagnosis. This decision itself is multifactorial with factors such as animal genetic merit, pregnancy status, expected calving date, and cow age being just some of the factors to consider when making the decision. Kelleher et al. (2015) collapsed all such information into a decision support tool for dairy females that they later termed C.O.W. index. The objective of C.O.W. is to rank individual dairy females based on their expected remaining lifetime profit potential. However, no such tool was available for beef females. Such a framework was developed in Chapter 5 and can be used for the same purpose, to rank females based on their expected remaining lifetime performance potential, albeit for beef females. Whilst the dairy C.O.W. was specifically tailored towards cows (i.e., animals that have had at least one calving), the Beef Female Profit Potential (BFPP; Chapter 5) is applicable to both heifers and cows. Thus, the BFPP can be utilised when choosing the most profitable beef heifers to retain within the herd as replacements as well as identifying animals that are candidates for culling. This is particularly useful when used in combination with the Transaction index (Chapter 5).

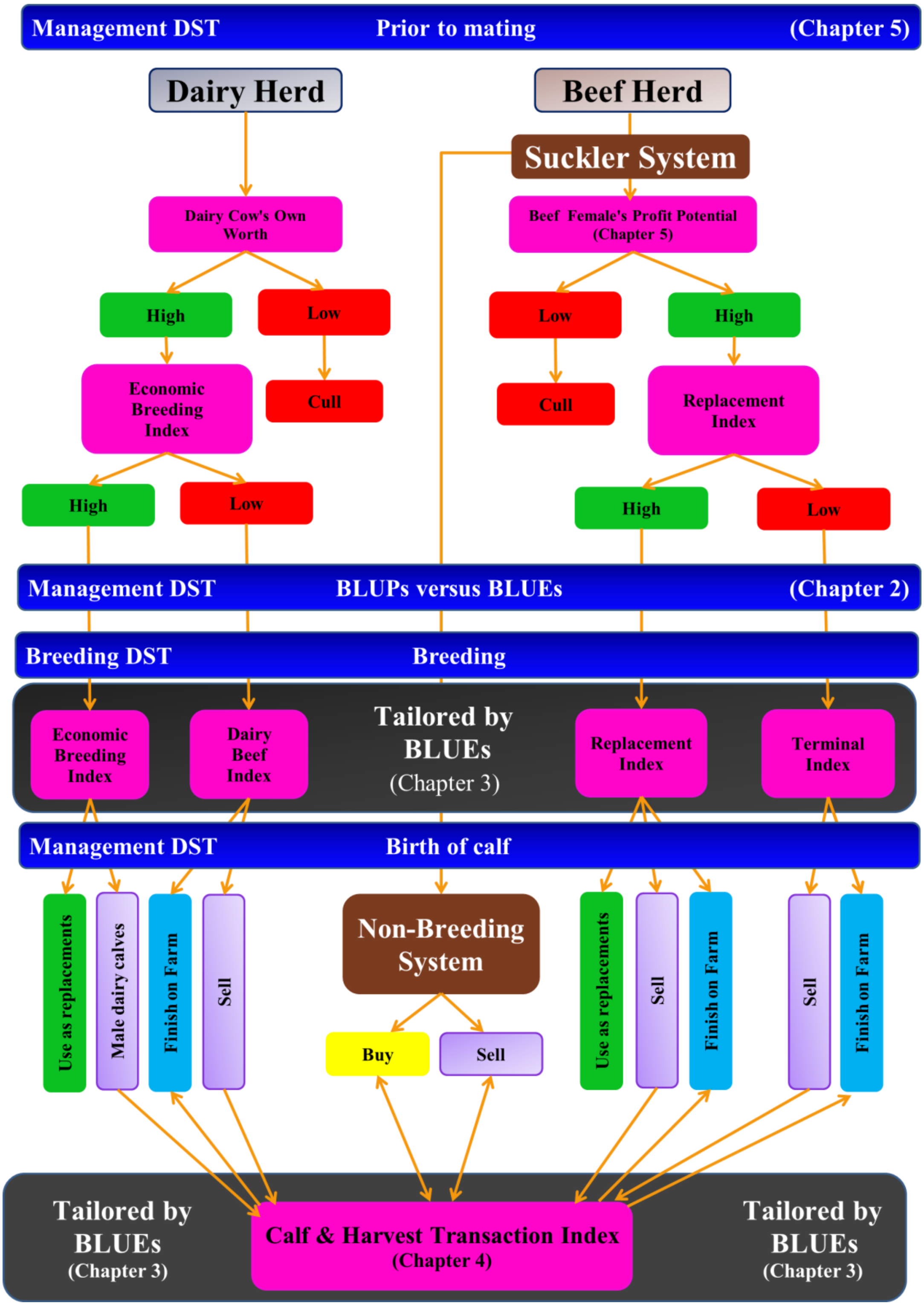

Figure 6.1: Description of the decision making process within the dairy and beef sector and how decision support tools (DSTs; pink boxes), both existing and novel DST developed in this thesis, can be utilised during main decision time-points (dark blue boxes) in the respective sector.

While the dairy C.O.W. and the BFPP indexes consider the animal's additive genetic merit, they also include estimates of non-additive genetic merit (i.e., heterosis and recombination) and non-genetic effects such as the cow parity effects, her age and permanent environmental effects. Furthermore, the framework developed facilitates the future potential inclusion of both additional traits (e.g., environmental footprint, animal health) but also more complex measures of the underlying components (i.e., better predictive analytical approaches such as machine learning based on more granular longitudinal data from sensing systems). For example, the heterosis coefficient estimates of animals included in both the dairy and beef C.O.W. indexes are solely based on expectations as defined by VanRaden and Sanders (2003), i.e., one less the sum of the breed proportion in the sire and dam for a particular breed; however, with the advent of genomic best linear unbiased prediction (GBLUP), it is possible to estimate individual dominance variance. Genomic heterozygosity can also be calculated per individual and fitted as a covariate in the genetic evaluation model replacing the expected heterozgosity in the model. Although heterotic effects have been relatively ignored in the past as they are not cumulative or persistent over generations, the inclusion of such estimates can improve the accuracy of animal merit predictions. Genomic estimations of dominance variance have been reported to account for between 3.8 to 7.1 % of the total phenotypic variance for production traits and 1.2 % of the total phenotypic variance for calving interval in dairy Holstein cows (Aliloo et al., 2016). Such estimates could potentially be extremely beneficial if incorporated into indexes such as the dairy C.O.W. and BFPP indexes as they can reward animals that are estimated to have additional heterotic effects more accurately which will impact their expected remaining lifetime profitability. In addition to this, given that maternal heterosis coefficients were included in the BFPP, the substitution of such effects with genomic estimates could provide more accurate estimations of the additional benefit a particular beef dam may have on her progeny, which will also ultimately impact her ranking on the BFPP index.

The incorporation of BLUEs into the dairy C.O.W. and BFPP DSTs also creates a unique opportunity for the natural progression of the current DSTs to become more precise DSTs, bespoke for individual herds based on their BLUEs. Firstly, when EBVs are estimated, it is assumed that a one-unit change in EBV will equate to a one-unit change in the respective trait; this assumption, however, generally only comes to fruition when animals are managed in an average environment. As demonstrated in Chapter 3, deviations from this expectation exist conditional on the BLUE of the herd. For instance, results from Chapter 3 demonstrated the response to selection on genetic merit for calving interval in a herd with a good BLUE for calving interval is over four times less relative to a herd with a poor BLUE for calving interval. Hence, it would be logical that BLUEs would be utilised within the available DSTs, largely because the necessary information and data actually already exists. In turn, such bespoke indexes would be more applicable and accurate or precise for a given herd. Lindblom et al. (2017) defined precision agriculture, relative to crop production, as a management concept that includes observing, measuring and responding to variability that occurs within the field. Thus, rather than treating the national herd environment as a homozygous entity, it makes sense to exploit herd BLUEs as a readily-available indicator of variability within the national herd thus facilitating herd managers to respond to such variability with tailored herd-specific decisions. The use of both the dairy C.O.W. and the BFPP DSTs in the respective sectors facilitate the identification of cows that are: 1) the least profitable in the herd that should be culled (Figure 6.1; red box) and, 2) the most profitable in the herd and therefore should be considered for breeding (Figure 6.1; green box). As the BFPP (Chapter 5) also estimates a heifer's expected lifetime profit potential, it is possible to identify the most profitable heifers to retain as replacements. Candidate breeding females can then be assessed using either the EBI (for dairy) or the Replacement index (for beef) in order to determine whether the females should be bred to produce replacements (i.e., if they have a high index value, Figure 6.1; green box) or progeny destined for slaughter (i.e., if they have a low index value, Figure 6.1; red box).

6.2.1.3 Decision support time-point: BLUPs versus BLUEs

As herd BLUEs already quantify the herd's management metrics independent of the its genetic merit, it is possible to use such information as a stand-alone tool for identifying traits that producers may be excelling in or performing sub-optimally. Thus, BLUEs have the potential to become the front line metric used in deciphering whether the herd's management system or genetic merit is negatively affecting performance (Figure 6.1). Farm extension services could exploit such information and use BLUEs as a tool to quickly identify key areas in which the client's production system should be improved. Furthermore, the associations between BLUEs and particular management characteristics discussed in Chapter 2 offer the opportunity to diagnose why a herd may be performing the way it is. For instance, if a herd has a poor calving interval, it may not necessarily mean the reproductive management in the herd is poor. Results from Chapter 2 suggest that longer calving intervals were associated with rapidly expanding herds relative to herds undergoing slow expansion as well as herds that purchase more animals rather than breed replacements. These results suggest that if a herd environment is undergoing a transient period of rapid expansion, and is purchasing in a lot of stock, calving interval may shorten once this growth phase is over and expansion rate slows; therefore in such herds, the longer calving interval performance is not a cause for concern in the long-term, rather a reflection of the current temporary situation. On the other hand if the herd has an excellent BLUE for calving interval, and has average calving interval phenotypic performance, then the herd may have a poor overall genetic merit for calving interval, which could suggest that the excellent management of the animals is compensating for poor genetic merit.

6.2.1.4 Decision support time-point: Breeding

At breeding, subscription services such as HerdPlus operated by ICBF provides access to breeding index data on individual animals within the herd, offering an opportunity for producers to select the most suitable dairy and beef bulls from an active list. The active bull list presents all available artificial insemination (AI) bulls from the various AI companies and displays the index value for each bull. Again, it is not unreasonable to consider an additional option that offers access to a bespoke active bull list whereby the relative herd BLUE regression coefficients (Chapter 3) are applied to the index values (e.g., the EBI or Terminal index), and subsequently personalised breeding goals are displayed. The application of the herd BLUE regression coefficients should be relatively simple as it involves only applying a multiplication factor to the already estimated EBVs and then summing the factors up; this can easily be disseminated via the HerdPlus web service since each HerdPlus account is unique to each farmer. Further customisation of the breeding goal could be possible by altering the economic weights on the traits so that they are specific to the production system; for example, full-time farmers with bigger cows may opt to reduce the weighting on calving difficulty genetic merit of the bull compared to part-time farmers with smaller cows.

Despite the abundance of information contained within the currently available breeding indexes as well as their capacity to assist in the identification of superior parents of the next generation, decisions about which female to mate to which male can become extremely complex and unwieldy. One DST to aid in the mating decisions is a mating advice tool. A Sire Advice web service was recently deployed by the ICBF within Herdplus (Carthy et al., 2019). A sire advice system currently only exists for dairy-dairy matings and therefore there is a void in a sire advice system for mating beef bulls to both dairy cows and beef cows. Given that it is common practice to mate a proportion of the dairy herd to beef bulls in Ireland, and as this practice is anticipated to increase, the demand for such a DST is only increasing (Berry and Ring, 2020). For example, based on an analysis of 6,358 Irish spring-calving dairy herds, older cows have a greater probability of being mated to beef bulls relative to younger cows (Berry and Ring, 2020). Despite this common practice in Ireland, no such DST currently exists that would aid in the mating of beef bulls to individual dairy females under the constraints (e.g. calving difficulty) imposed by the farmer. There is also scope for additional information to be included in such DST such as incorporating estimates of dominance. Aliloo et al. (2016) reported that as a result of including non-additive genetic effects within mating programs, the progeny of Holstein dairy cows were, on average, $8.42 (based on an index which incorporated both fertility and production traits) more profitable, relative to the progeny arising from a model that was based only on additive genetic merit. Benefits from the inclusion of non-genetic effects within mating programs are not justifiably confined to animals that will be retained as replacements in the dairy herd. Dominance genetic variance for traits such as intra-muscular fat and carcass retail beef yield have been reported to be 10 % and 18 % of the total phenotypic variance, respectively (Bolormaa et al., 2015). Therefore, this suggests that with the incorporation of dominance effects in a mating program, the combining ability of mating pairs can be exploited when breeding the proportion of the herd that will be finished for beef production. For such animals, the persistence of the heterosis effects over generations is irrelevant as the progeny never become parents. Nevertheless, as the transaction index (Chapter 4) incorporates heterosis effects, the increased benefit due to heterosis will be reflected in the index value and producers can command higher prices for their growing animals.

6.2.1.5 Decision support time-point: birth of calf

Once the calf is born, a decision needs to be made whether to retain the calf as a replacement (Figure 6.1; green box), to finish the calf on the farm (Figure 6.1; light blue box) or sell the calf for beef production (Figure 6.1; purple and yellow box). For males, the latter two options are often the choice but the decision must be made for the females. Given the multi-functional nature of the developed transaction index in Chapter 4, the information is not only pertinent in facilitating the transaction of animals, but can also give producers who have young females the opportunity to assess the calf's relative predicted carcass revenue. In addition to this, producers can also utilise the BFPP (Chapter 6) at this point to consider the female calf's expected predicted lifetime profit potential if she was retained in the herd as a replacement. Thus, producers have the opportunity to make an informed decision based on whether to keep the calf as a replacement or finish her for beef production. For example, a female calf may have high BFPP value (Chapter 6) combined with a low transaction index value (Chapter 5) and therefore should be retained as a replacement. There is potential for producers who wish to buy and sell replacements, to then utilise the BFPP as an indicator of the beef female's worth. Whereas if the calf has a high transaction index value and is therefore destined for beef production, the transaction indexes can be utilised when trading the animals.

In the past, the value placed on calves in livestock auctions has predominantly been based on their estimated breed composition; however with the availability of crossbred animals increasing, it may no longer be possible to accurately predict the breed of an animal based on their observed coat colour. Because of mendelian sampling during gametogenesis, it is not possible to know the breed composition of an animal from a crossbred parent without exploiting genomic information. Since 2016, calf registrations originating from the dairy herd have increased year-on-year; a major consequence of which is the increasing number of calves for sale originating from the dairy herd (Figure 6.2) with a growing proportion being dairy × beef calves.

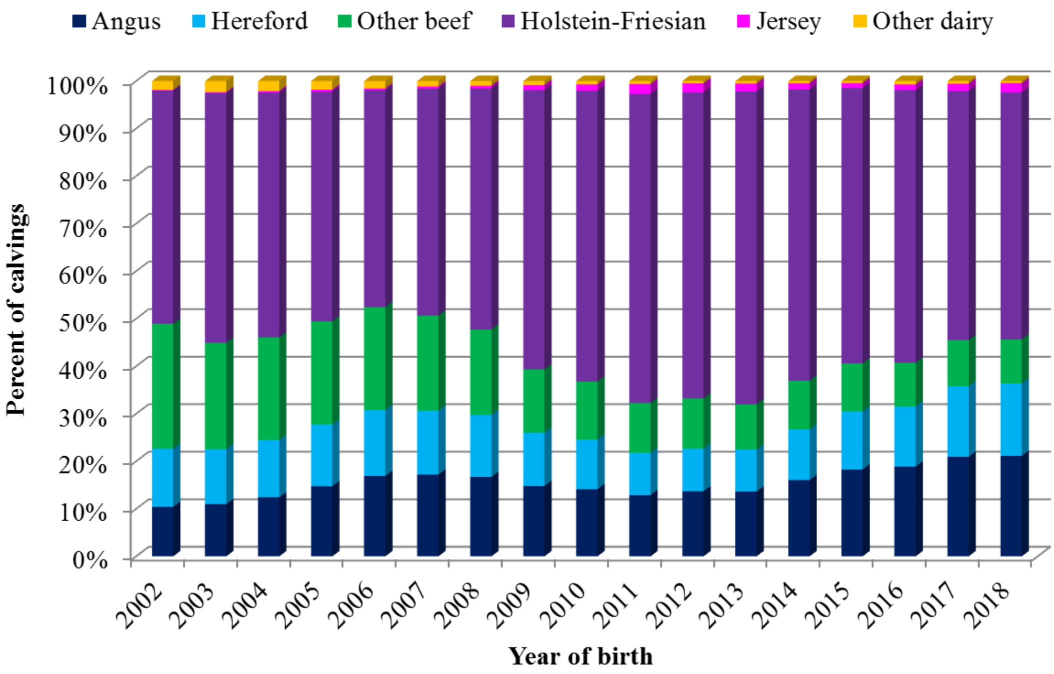

Figure 6.2: A representation of sire breeds by year of birth to Irish Holstein-Friesian dams in Ireland as reported in Berry and Ring (2020b).

The proposed transaction indexes (Chapter 4) offer the unique opportunity for increased transparency when trading cattle and for the end-user to rely on scientifically-backed predictions of carcass revenue rather than looks when valuating an animal. There is also an opportunity for the transaction indexes to be further tailored to the finishing herd's production system using BLUEs (Chapter 3). Although this thesis focused on BLUEs for fertility and milk production traits, the same concept of modifying the EBVs underlying the indexes depending on the herd's BLUE for carcass traits could also be applicable to the beef DSTs; if the same phenomena existed for carcass traits, then there may also be a justifiable case to incorporate such sensitivity in the expression of genetic merit to environment within the transaction indexes developed in Chapter 4. One such way of doing this would be at the livestock auction, the transaction index value of the calf within the average environment could be displayed on the livestock auction board, and a bespoke transaction index value could be adapted and displayed via a HerdPlus app for each farmer individually. Furthermore, the development of the internet of things (IoT) has opened up avenues for data collection at every possible point along the production system. In the future by utilising new technologies as they come available, it may be possible to: 1) weigh (or predict the weight) the animals on their arrival to the auction, 2) input the animal's sex (i.e., female, bull, steer), 2) upload Blockchain verified weight phenotypes to the service provider such as ICBF and, 3) provide updated, more accurate real-time estimates of the transaction index values to the potential buyers on the day of the auction. It may also be possible to adjust the transaction value for costs such as feed that will be incurred for the estimated duration of the animal's lifetime. The Calf index is directed towards producers who specialise in purchasing young calves for the purpose of growing and either finishing the calves themselves, or will sell them on to a specialised finisher facility. In such an index, consideration must also be given to both docility and feed intake especially given that feed costs are the largest variable input costs in cattle production (Montano-Bermudez et al., 1990). The phenotypic SD for feed intake among the validation animals in the Chapter 4 was 1.76 kg DM/day while the SD for the Calf transaction index (i.e., calculated using PVs) was €69.14; given the correlation of -0.22 between the two, animals in the top 20% of the population for the Calf transaction index were expected to eat, on average, 0.54 kg DM/d less than the average animal who was eating 13.09 kg DM/d; this represents a difference of 0.31 SD units. Assuming a constant differential of 0.31 SD over a 120-d finishing period, this saving would be expected to accumulate to a reduction in feed intake of 65.20 kg DM and, based on a cost of €0.29 / kg DM, this equates to a saving of almost €20 per animal (just over the finishing period). The SD for feed intake, however, does not remain consistent across the animal's lifetime. From a meta-analysis review of the literature in cattle, as well as from data used in Chapter 4, the published SD for DMI of growing cattle was plotted against age in Figure 6.3 (Myers et al., 1999; Wang et al., 2006; Kelly et al., 2010a; Kelly et al., 2010b; Kelly et al., 2011; Khan et al., 2012; Durunna et al., 2013). A linear regression line was subsequently fitted ($R^2 = 0.62$) to the data regressing the SD of DMI on age with regression model being:

$$\mathrm{SD}_{DMI} = 0.6975 + 0.0018 \times \mathrm{age}$$

Assuming the calculated relative difference of 0.31 SD units in DMI between the top 20% of animals on PV versus the those average on PV remains the same throughout life, it was possible to estimate the expected kg DM difference in DMI per day from the linear regression model solutions for each day of age (Figure 6.4). The validation population in Chapter 4 were, on average, 548 days of age at harvest (at the end of their test).

Therefore, if purchased at 248 days of age (i.e., 300 days of feeding), it is estimated that animals in the top 20 % stratum would eat just under 132 kg DM less than the average, equating to a saving of €38; assuming a price of €0.29 per kg of DM. If the animals were, however, only purchased 100 d prior to harvest, the saving would only be €14.41. Therefore, given the variation in feed cost, there is potential for such savings to be represented within the transaction index. Furthermore, feed intake has been reported to be a factor with a strong association with enteric methane in dairy cows (Lassen and Løvendahl, 2016). Although traits pertaining to greenhouse gas emissions are not explicitly included in any cattle breeding program as they are currently not of economic importance (de Haas et al., 2017), given the growing awareness surrounding agriculture's environmental 'hoofprint', it is possible that this may change with carbon costs of €80 / tonne being touted; this change could be reflected in an increase in the value of the top 20 % of animals on PV versus the those average on PV as they ate less, and therefore could potentially produce less enteric methane.

An opportunity also exists for growing animals to be traded under a brokerage system using the transaction index as an indicator of the value the animal is worth. This would mean that traders or the animals themselves would not need to enter livestock auctions, which would in turn place less stress on the animal as well as reduce biosecurity risks. Moreover, the transaction index can also be utilised in situations such as Covid-19, whereby the movement and gathering of individuals may be restricted. The index itself has been developed to be dynamic and adaptable to the inclusion of even more informative data metrics such as regional genomic estimates of heterozygosity and novel IoT phenotypes.

Once animals have been traded and finished using the transaction index, or have been identified for retention within the herd using the BFPP index, the process begins again within the breeding herds. And once again both dairy and beef females must be partitioned into the females that will be used to breed future replacements, animals for beef production, or those themselves that will be culled and removed from the herd. Ultimately, the information gathered and the DSTs developed within this thesis provide the opportunity to improve upon the decision process currently available and provide a greater level of tailored support to producers at key decision time points along the production chain.

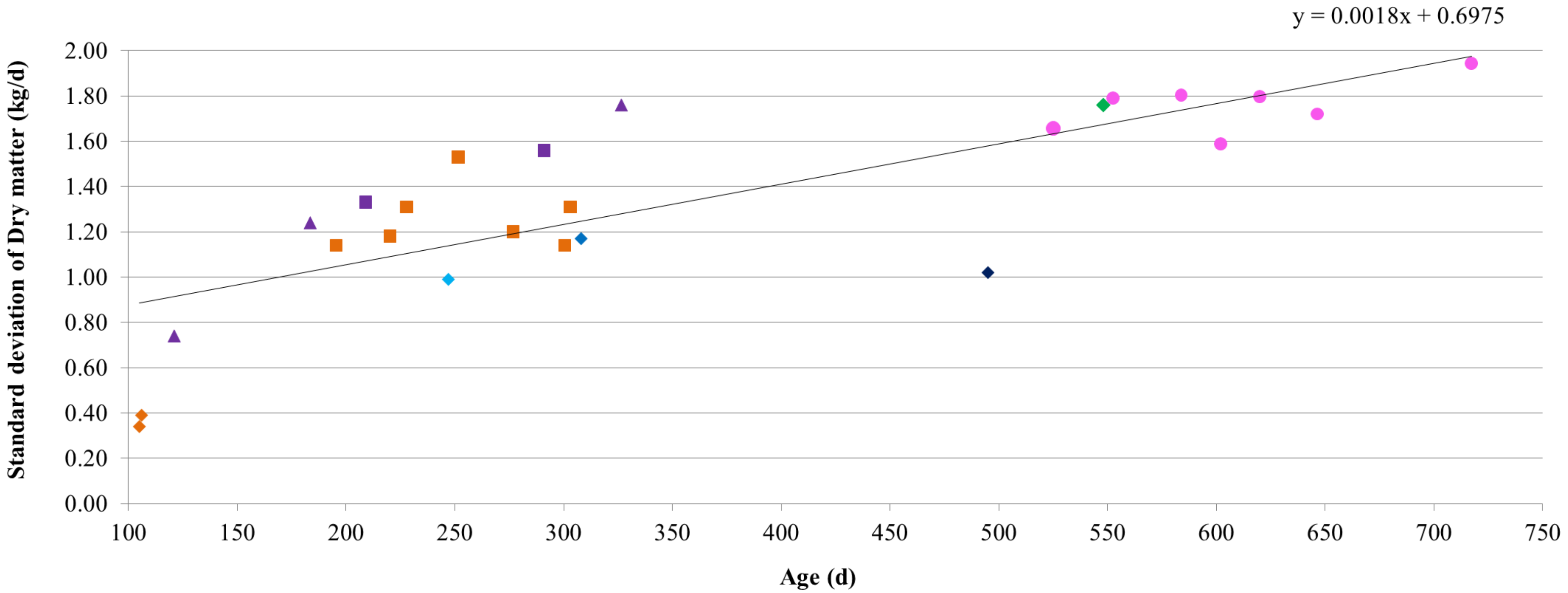

Figure 6.3: Standard deviation of dry matter intake (kg/d) corresponding to the reported age of animals in Khan et al. (2012) (orange diamond), Myers et al. (1999) (purple triangle), Wang et al. (2006) (orange square), Durunna et al. (2013) (purple square), Kelly et al. (2010a) (light blue diamond), Kelly et al. (2011) (blue diamond), (Kelly et al., 2010b)(navy diamond), average feed intake SD using Tully feed intake performance data when ranked on age (pink circle) and, the present study (green diamond) as well as equation of the line.

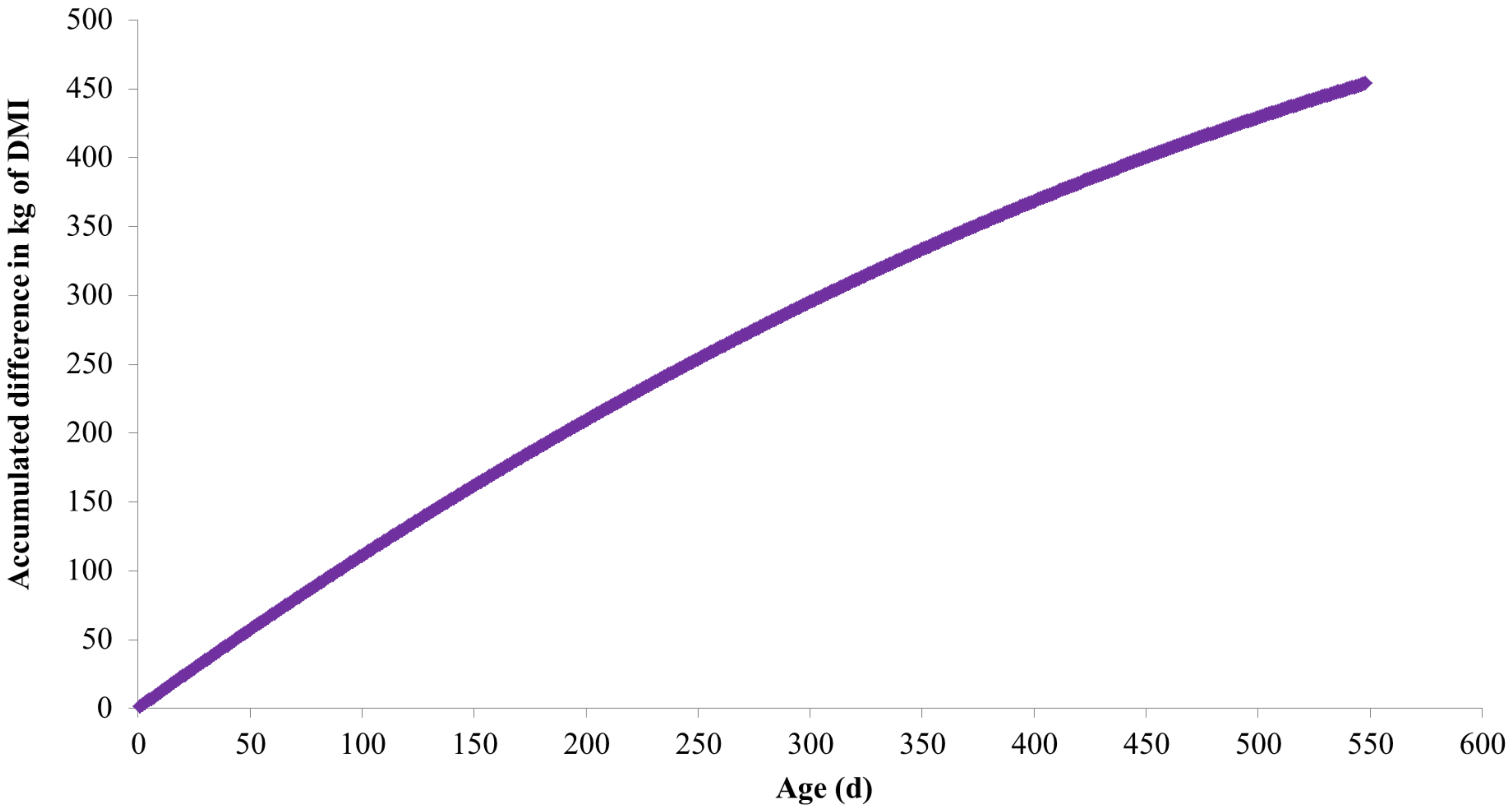

Figure 6.4: The accumulating difference in the standard deviation of dry matter intake (kg of DMI) between animal in the top 20% for the Calf index and the average as the animal ages.

6.3 Further Research

Irrespective of the species, genetic evaluations simultaneously generate both BLUEs and BLUPs. Therefore, not only is there global potential to incorporate BLUEs into DSTs, but the actual traits considered can be expanded from those used in this thesis and also can be applied to other domesticated species (e.g., sheep, pigs). For example, strict beef carcass specifications are enforced in Ireland through the use of the EUROP grading system in order to meet consumer demand for optimally sized primal carcass cuts. BLUEs have the potential to be used as an identifier of herds that are consistently failing to meet the required grades specified by the processors. Moreover, as the availability of health data becomes accessible, and as health traits get included in genetic evaluations, BLUEs could be calculated for herds which, in turn, could be used to identify herds that are more predisposed to disease and this information could provide indications of disease hot-spots around the country. The opportunity also exists to quickly identify herds that are having difficulties with important animal welfare related traits, such as calving difficulty or perinatal mortality, using BLUEs. Herd BLUEs can be exploited as an alert indicator of systematic sub-optimal performance which could potentially link to an extension service that can provide tailored management advice to each farmer.

As the availability of technology continues to grow under the umbrella of the internet of things, there will be endless possibilities as to how novel phenotypes can be measured as well as how such information can feed back into DSS. Distributed ledgers such as Blockchain also offers a unique method to achieve transparency and provenance across the entire production system whereby any authorised stakeholder could trace back through the entire production system and obtain (verified) information on each individual animal. This information could potentially include the genomic estimates of breed composition, the quality of colostrum received as a calf (which can now be measured with saliva sample; Johnsen et al., 2019), vaccination statuses and movement reports. The inclusion of health-related data within the transaction index developed (Chapter 4) could provide the added benefit of identifying trends relative to calf vigour and vitality, as well as provide an opportunity to identify potential reasons as to why some calves fail to sell. Furthermore, as the transaction index is tailored towards animals that are destined for beef production, and will ultimately end up on the shelves of retail outlets, simplified versions of such information could also be made available to customers. For instance, customers may have more confidence in the quality of the product and may be willing to pay a premium from knowing the primary diet of the animal (e.g., 75% grass-fed) and the county in which the animal was finished in. Moreover, there is scope for further investigation into the potential benefits of incorporating genomic information to better estimate not only parentage, but also breed composition and non-additive genetic effects (dominance, heterozygosity and inbreeding coefficients); all of which can ultimately feed into the DSTs proposed in this thesis and, in turn, provide more information and assist further in the decision making process.

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7.1 References

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Chapter 8: Publications and Contributions from this Thesis

8.1 Peer Reviewed Publications

Dunne, F. L., M. M. Kelleher, S. W. Walsh, and Berry, D. P., 2018. Characterization of best linear unbiased estimates generated from national genetic evaluations of reproductive performance, survival, and milk yield in dairy cows. Journal of Dairy Science, 101(8), p. 7625–7637.

Dunne, F. L., S. McParland, M. M. Kelleher, S. W. Walsh, and D. P. Berry. 2019. How herd best linear unbiased estimates affect the progress achievable from gains in additive and nonadditive genetic merit. Journal of Dairy Science, 102(6):5295-5304.

Dunne, F. L., R.D. Evans, M. M. Kelleher, S.W. Walsh, and D. P. Berry. 2020. Formulation of a decision support tool incorporating both genetic and non-genetic effects to rank young growing cattle on expected market value. Animal. Submitted.

Dunne, F. L., D. P. Berry, M. M. Kelleher, R. D. Evans, S. Walsh, and P. R.Amer. 2020. Formulation of a decision support tool incorporating both genetic and non-genetic effects to rank young growing cattle on expected market value. Journal of Animal Science. Submitted.

8.2 Conferences

Dunne, F. L., Kelleher, M. M., Walsh, S. W. & Berry, D. P., 2018. Characterization of best linear unbiased estimates generated from national genetic evaluations of reproductive performance, survival, and milk yield in dairy cows. The British Society of Animal Science Conference, Dublin, Ireland.

Dunne, F. L., S. McParland, M. M. Kelleher, S. Walsh, and D. P. Berry. 2018. Management Metrics – Are you achieving your genetic potential? Irish Cattle Breeding Federation and Sheep Ireland Genetics conference, Athlone, Co. West Meath, Ireland.

Dunne, F. L., R. D. Evans, M. M. Kelleher, S. McParland, S. Walsh, and D. P. Berry. 2019. Decision-making, made easy. Vista Milk Conference, Carlow, Co. Carlow, Ireland.

Dunne, F. L., R. D. Evans, M. M. Kelleher, S. McParland, S. Walsh, and D. P. Berry. 2020.

Providing transparency in times of uncertainty. Irish Cattle Breeding Federation and Sheep Ireland Genetics conference, Co. Kildare, Ireland.

8.3 Other Publications

Carthy, T. R., Kelleher, M. M., **Dunne, F. L.**, Berry, D. P. 2018. New value-adding tools. TResearch Vol.13, Number 1, p.18-19. Spring 2018. https://www.teagasc.ie/publications/tresearch

Carthy, T. R., Kelleher, M. M., McCarthy, J., **Dunne, F. L.** 2019. Decision support tools: what your data can do for you. Moorepark Irish Dairying, Growing Sustainably, p.194-195. July 2019. https://www.teagasc.ie/media/website/publications/2019/Moorepark19-Irish-Dairying-booklet.pdf

8.4 Industry Dissemination

Dunne, F. L. 2018. Developing decision support tools from genetic evaluations. In: Waterford Institute of Technology guest lecture. Waterford, Ireland. 26-Nov-2018

Dunne, F. L. 2019. Genetic Evaluations – Decision Support Tools. In: Munster Bovine Genetics. Mallow, Co. Cork, Ireland. 26-Feb-2019

Dunne, F. L. 2019. Making the most from genetic evaluations. In: Teagasc, Munster Bovine Genetics and ICBF industry meeting. Fermoy, Co. Cork, Ireland. 21-Mar-2019

Dunne, F. L. 2019. Decision Support Tools. In: Vista Milk Governance meeting. Mallow, Co. Cork, Ireland. 22-May-2019

Dunne, F. L. 2019. Beef index development. In: ICBF Technical advisory group meeting. Dublin, Ireland. 11-June-2019

Dunne, F. L. 2019. Best Linear Unbiased Estimates. In: ICBF Technical advisory group meeting. Dublin, Ireland. 11-June-2019

Dunne, F. L. 2019. Transaction Index. In: Meat Technology Ireland meeting. Fermoy, Co. Cork, Ireland. 09-July-2019

Dunne, F. L. 2019. The calf transaction index. In: ICBF industry meeting. Bandon, Co. Cork, Ireland. 30-Aug-2019

Dunne, F. L. 2019. Developing decision support tools from genetic evaluations. In: Abacusbio. Dunedin, New Zealand. 16-Sept-2019

Dunne, F. L. 2020. Beef's Own Worth. In: ICBF Technical advisory group meeting. Dublin, Ireland. 07-Jan-2020

Dunne, F. L. 2020. Beef's Own Worth transaction index. In: Vista Milk monthly meeting. Fermoy, Co. Cork, Ireland. 21-Jan-2020

8.5 Research Awards

Walsh Fellowship International Training Award 2019. Travel bursey to visit Abacusbio in Dunedin, New Zealand. Working under the supervison of Dr. Peter Amer. September to December 2019.

The Brian Wickhan Award for 'Best Poster' 2020. Travel bursary valued at €500 awarded for 'Best Poster' at the Irish Cattle Breeding Federation and Sheep Ireland genetics conference. 16-Jan-2020

8.6 Courses Attended

How to do the Literature Review (Science and Engineering)
WIT; 29th November 2017

Topics explored in this course included scientific writing, expectations as well as guidelines when writing a literature review, Endnote as a referencing tool, refining researching techniques and methods of developing a repertoire of vocabulary. This course was conducted through a lecture.

Leadership skills for Agri-Food Researchers
UCC (AFGDP course); 17th – 19th January 2018

Topics covered in this course included developing the tools to improve leadership skills and team working skills, networking, effective communication, presenting, managing conflict, providing and receiving feedback as well as carrying out DiSC and Belbin analysis. This course was conducted through lectures, exercises and self-study sessions.

NOVA course on 'Quantitative Genetics Applied in Animal Breeding'
Mikkeli, Finland; 06th – 10th August 2018

This course covered topics which covered how quantitative genetics is applied in animal breeding, the background methodology of quantitative genetics as well as the use of analytics software, especially R, in quantitative genetics. This course was conducted through lectures, exercises and self-study sessions.

Practical pedagogy

WIT; February to April 2018

Topics explored in this course included methods of class engagement, setting learning goals, the basic principles of preparing the material and the method of delivering the material to the class, teaching the class and finally, evaluating the students' progress. This course was conducted through lectures, micro-teaching sessions, exercises and self-study sessions.

Chapter 9: Supplementary Material, Tables and Figures

9.1 Supplementary Material

Supplementary Material S9.1: Statistical models used in the carcass, docility and calving genetic evaluations were as follows:

$$Carcass\ trait_{deghijklmz} = \sum_{a=1}^{4} Het_z + \sum_{b=1}^{16} Breed_z + \sum_{c=1}^{3} age_z^c + twin_{zd} + byr_{ze} + AbattoirCG_{zf} + \sum_{g=1}^{2} HY_z + dam\ fraction_{zh} + dam\ age_{zi} | dam\ parity_{zj} + dam\ pe_{zk} + \ animal_{zl} + residual_{zm}$$

$$Feed\ intake_{dehnhijlm} = \sum_{a=1}^{4} Het + \sum_{b=1}^{16} Breed + \sum_{c=1}^{3} age^c + twin_d + byr_e + HYS_n + dam\ fraction_h + dam\ age_i | dam\ parity_j + \ animal_l + residual_m$$

$$Liveweight_{dephijkolmx} = \sum_{a=1}^{4} Het_x + \sum_{b=1}^{16} Breed_x + \sum_{c=1}^{3} age_x^c + twin_{xd} + byr_{xe} + \sum_{g=1}^{2} HY_x + dam\ dairy\ fraction_{xh} + dam\ age_{xi} | dam\ parity_{xj} + dam\ pe_{xk} + sex_{xo} + \ animal_{xl} + \ residual_{xm}$$

$$Docility_{aqnjolm} = \ Het_a + \sum_{b=1}^{16} Breed + \sum_{c=1}^{2} age^c + Recomb_q + HYS_n + dam\ parity_j + sex_o + \ animal_l + \ residual_m$$

$$Calving\ traits_{enijkoymly} = \sum_{a=1}^{4} Het_y + byr_{ye} + HYS_{yn} + dam\ age_{yi}|dam\ parity_{yj} + dam\ pe_{yk} + sex_{yo} + animal_{yl} + residual_{ym}$$

$Carcass\ trait_{deghijklmz}$ = carcass trait *z* (i.e., weight [kg], conformation and fat [scale of 1 to 15]); $Feed\ intake_{dehnhijlm}$ = feed intake (kg DM/day); $Liveweight_{dephijkolmx}$ = live-weight (kg) trait *x* (recorded between the ages 150 d and 250 d old (weanlings), between 251 d and 350 d old (adolescent), between 351 d and 450 d old (adult), and between 451 d and 550 d old (finisher)); $Docility_{aqnjolm}$ = docility (scale 1 (docile) to 5 (difficult)); $Calving\ traits_{enijkoymly}$ = calving trait y (i.e., calving difficulty (scale 1 to 4), mortality (%) and gestation length (days); Het = heterosis coefficient which is fitted as four separate heterosis coefficients to represent different breed crosses within the carcass trait and feed intake genetic evaluation and is fitted as a single coefficient a in the docility genetic evaluation; $Breed$ = covariate representing the proportion of 16 breeds (i.e., Aberdeen Angus (AA), Aubrac (AU), Blonde D'Aquitaine (BA), Belgian Blue (BB), Charolais (CH), Friesian (FR), Hereford (HE), Holstein (HO), Jersey (JE), Limousin (LM), Piemontese (PI), Montbelliarde (MO), Parthenais (PT), Salers (SA), Shorthorn (SH) and Simmental (SI); age^c = age of the animal (linear, quadratic and cubic for all traits except for docility which included linear and quadratic age) at the time of slaughter for carcass traits (i.e., weight, conformation, fat, feed intake recording for feed intake trait, or docility scoring for docility trait; $twin_d$ = whether or not the animal was a twin; byr_e = birth year of the animal *l*; $AbattoirCG_{zf}$ = the covariate representing the abattoir contemporary group *f* coefficient pertaining to trait *z*; HY_g = herd year contemporary group coefficient g of: 1) carcass traits *z* (includes contemporary group coefficient for herd that animal *l* was harvested in and the previous herd that animal *l* spent the most time in) and, 2) live-weight *x* (includes contemporary group coefficient for herd that animal *l*'s live-weight was recorded in and the previous herd that animal *l* spent the most time in); and HYS_n = herd year season contemporary group coefficient n of: 1) feed intake recording, 2) docility recording, 3) calving traits *y*; $dam\ dairy\ fraction_h$ = dam dairy breed fraction coefficient *h*; $dam\ age_i|dam\ parity_j$ = the interaction between dam age *i* and the dams

jth parity (i.e., 1 to 7, inclusive) for all traits with exception to docility whereby just the dams jth parity is modelled; dam pe_{k}= permanent environment effect k of animal l's dam; sex_o = whether animal l was male or female for docility evaluation, otherwise, bull, steer or heifer; $Recomb_q$ = recombination coefficient, $animal_l$ = direct genetic effect of animal l, and $residual_m$= residual term.

9.2 Supplementary Tables

Supplementary Table S9.1: Classification of the five strata describing the six herd-level characteristics, including population breakdown of sub-categories for herd size and herd-level use of AI corresponding to the specific herd-year best linear unbiased estimates for age at first calving (AFC), calving to first service interval (CFS), number of services (NS), calving interval (CIV), survival (SU) and milk.

	Category				
Herd-level characteristics	1	2	3	4	5
Herd size (no. of animals)	very small	small	average	large	very large
CFS, SU, NS, AFC	< 50	50-64	65-79	80-109	≥ 110
CIV, Milk yield	< 65	65-74	75-89	90-109	≥ 110
Rate of expansion (no. of animals)	0	1-3	4-6	7-8	≥ 9
Proportion of home-born animals (%)	< 70	70-79	80-94	95-99	100
Herd-level use of AI (%)					
NS	< 75	75-79	80-84	85-94	≥ 95
CFS, SU	< 55	55-69	70-79	80-89	≥ 90
AFC, CIV, Milk yield	< 45	45-69	70-79	80-89	≥ 90
Proportion of breed society registered animals (%)	0	1-4	5-34	35-95	> 95
Calv 42 (%)	< 50	50-59	60-69	70-80	> 80

Supplementary Table S9.2: Linear regression coefficients of phenotypic performance for each trait on the heterosis coefficients pertaining to various crosses including Holstein Friesian (HO × FR), Holstein × Jersey (HO × JE), Holstein × Montbelliarde (HO × MO), Holstein × Meuse Rhine Yssel (HO × MY) and Swedish Red × Holstein-Friesian (SR × HF) within each herd best linear unbiased estimate stratum including the significance of the interaction.

		Herd Rank		
BLUEs trait	Best	Average	Worst	P-value
Age at first calving (d)				
HO × FR	-3.08 (2.88)	-2.70 (2.65)	4.54 (2.74)	
HO × JE	-3.98 (2.58)^{a}	-7.12 (3.13)^{ab}	-14.53 (4.34)^{b}	*
HO × MO	-2.72 (17.16)	-4.36 (9.50)	-30.54 (10.96)	
HO × MY	-17.52 (19.54)	-15.69 (14.22)	-31.06 (9.38)	
SR × HF	-4.25 (4.17)	-4.67 (3.78)	-21.40 (5.40)	
Milk yield (kg)				
HO × FR	180.34 (15.96)^{a}	224.09 (16.08)^{a}	336.06 (16.12)^{b}	***
HO × JE	48.62 (30.34)^{a}	212.60 (21.87)^{b}	151.36 (14.89)^{c}	*
HO × MO	422.08 (65.22)	471.48 (63.76)	442.13 (47.41)	
HO × MY	-51.93 (77.22)^{a}	527.29 (83.28)^{b}	264.69 (60.66)^{c}	***
SR × HF	33.84 (38.32)^{a}	222.08 (27.32)^{b}	55.81 (26.55)^{a}	***
Survival				
HO × FR	0.01 (0.01)^{a}	0.02 (0.01)^{a}	0.04 (0.01)^{b}	***
HO × JE	0.03 (0.01)	0.04 (0.01)	0.04 (0.01)	
HO × MO	0.02 (0.03)	0.04 (0.02)	0.00 (0.02)	
HO × MY	0.05 (0.03)	0.01 (0.02)	0.02 (0.03)	
SR × HF	-0.01 (0.01)	0.02 (0.01)	0.03 (0.01)	*
Number of services (units)				
HO × FR	-0.03 (0.02)	-0.04 (0.02)	-0.09 (0.02)	
HO × JE	-0.05 (0.03)^{a}	-0.05 (0.02)^{a}	-0.12 (0.02)^{b}	***
HO × MO	-0.84 (0.07)	0.04 (0.06)	-0.12 (0.06)	
HO × MY	-0.02 (0.08)	-0.02 (0.06)	0.04 (0.08)	
SR × HF	-0.02 (0.04)	-0.05 (0.03)	-0.07 (0.02)	
Calving to first service interval (d)				
HO × FR	-0.60 (0.56)	-0.31 (0.49)	0.65 (0.52)	
HO × JE	2.75 (0.92)^{a}	0.13 (0.56)^{b}	-2.40 (0.51)^{c}	***
HO × MO	0.98 (2.0)	-0.56 (1.97)	-2.10 (1.70)	
HO × MY	0.83 (2.62)	-1.35 (2.44)	-0.41 (2.49)	
SR × HF	0.58 (1.29)	1.05 (0.80)	-0.27 (0.73)	
Calving interval (d)				
HO × FR	-0.82 (1.26)^{a}	-2.64 (1.09)^{a}	-9.77 (1.22)^{b}	***
HO × JE	-3.26 (1.91)^{a}	-3.31 (1.41)^{a}	-6.04 (1.42)^{a}	*
HO × MO	-4.93 (4.0)^{ab}	0.31 (4.35)^{a}	-15.04 (3.92)^{b}	*
HO × MY	-2.38 (4.32)	-3.76 (4.56)	-3.83 (4.90)	
SR × HF	-1.06 (2.41)	-3.71 (1.94)	-5.84 (2.77)	

Supplementary Table S9.3: Component traits of the different indexes evaluated, including the traits units of measurement, genetic standard deviation (SD) and economic weighting.

	Index					
Component trait	National Terminal	Calf	Harvest	Units	Genetic SD	Economic weight
Calving difficulty	✓	-	-	%	0.158	-€4.65
Calving mortality	✓	-	-	0 to 1	0.038	-€5.34
Gestation length	✓	-	-	Days	3.020	-€2.25
Docility	✓	✓	-	1 (very quiet) to 5 (very difficult)	0.365	€17.03
Feed intake	✓	✓	-	kg DM per day	0.667	-€38.63
Carcass weight	✓	✓	✓	Kg	15.419	€3.14
Carcass Conformation	✓	✓	✓	EUROP scale E (best) to P (worst)	0.644	€14.77
Carcass Fat	✓	✓	✓	1 (leanest) to 15 (fattest)	0.679	-€7.86

Supplementary Table S9.4: Quality based pricing grid displaying cent (€) per kg corresponding to the EUROP carcass classifications and fat grade awarded to the carcass.

	EUROP Classification														
Fat grade	E+	E=	E-	U+	U=	U-	R+	R=	R-	O+	O=	O-	P+	P=	P-
1-	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
1=	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
1+	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
2-	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
2=	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
2+	442	436	430	424	418	412	406	400	400	382	376	370	364	358	352
3-	442	436	430	424	418	412	406	400	400	388	382	376	370	364	358
3=	442	436	430	424	418	412	406	400	400	388	382	376	370	364	358
3+	442	436	430	424	418	412	406	400	400	388	382	376	370	364	358
4-	442	436	430	424	418	412	406	400	400	388	382	376	370	364	358
4=	442	436	430	424	418	412	406	400	400	388	376	370	364	358	352
4+	436	430	424	418	412	406	400	394	394	382	376	370	364	358	352
5-	418	412	406	400	394	388	382	376	376	364	358	352	346	340	334
5=	418	412	406	400	394	388	382	376	376	364	358	352	346	340	334
5+	418	412	406	400	394	388	382	376	376	364	358	352	346	340	334

Supplementary Table S9.5: The phenotypic records belonging to the validation population which were included amongst the remaining population in each individual carcass genetic evaluation iteration, whereby phenotypes encompass the traits carcass weight, carcass conformation, carcass fat and, feed intake phenotypic records. Live-weight phenotypes were recorded at 4 different age-points of the animals.

Genetic evaluation iteration	Phenotypes	Live-weight (d)			
		150-250	250-350	350-450	450-550
1	✓	✓	✓	✓	✓
2	-	-	-	-	-
3	-	✓	-	-	-
4	-	-	✓	-	-
5	-	-	-	✓	-
6	-	-	-	-	✓
7	-	-	✓	✓	✓

Supplementary Table S9.6: Annual cost associated with retaining a dry cow in the herd.

Cost type	Cost source	Cost of dry cow (€)
Cash costs	Concentrates	20
	Grassland (fertilizer, lime, reseeding)	52
	Machinery hire	14
	Silage making	156
	Replacement heifer	32
	Overheads[1]	111
Non-cash costs[2]	Depreciation on buildings and machinery	82
	Land charge for owned land	132
	Total costs	599

[1] Overheads costs refer to general operational costs pertaining to a car, phone, electricity, insurance, interest on loans, etc.

[2] Non-cash costs don't require cash payment every year

Supplementary Table S9.7: Components included in the cost estimation of rearing a heifer up to point of calving at 24 months old.

Heifer replacement cost to calving at 24 months		
Year	Cost source	Euro
Year 1	Grazed grass	40
	Grass silage	113
	Concentrates	32
	Vaccinations	12
	Vet/medicine	8
	Dosing	11
	Labour	131
	Fixed cost contribution	80
	Sub total (year 1)	*427*
Year 2	Grazed grass	141
	Grass silage	158
	Concentrates	48
	Vaccinations	12
	Vet/medicine	85
	AI/breeding	36
	Dosing	8
	Labour	61
	Fixed cost contribution	140
	Sub total (year 2)	*688*
	Total from calf-hood to calving	1116
	Mortality Rate	5%
	Cost including mortality	1174
	Plus cost of suckler cow	616
Total	Total cost of homebred replacement	1790

Supplementary Table S9.8: Least squares means for cull cow carcass weight after adjusting for carcass fat, carcass conformation, estimated breeding value for cull cow carcass weight and parity.

Parity	LSM	Standard Error
1	335.05	0.95
2	352.59	0.95
3	363.34	0.96
4	369.64	0.96
5	373.33	0.97
6	374.51	0.98
7	374.80	1.00
8	373.83	1.03
9	372.67	1.06
10	369.62	1.10

Supplementary Table S9.9: Survival transition matrix between consecutive parities given the animal's rank for survival and current parity month of calving group (MOCG) which are 1 (January), 2 (February), 3 (March), 4 (April), 5 (May), 6 (June), 7 (July and August), 8 (September), 9 (October to December).

Current parity		Probability of transitioning to next parity								
		Current parity month of calving group								
Parity	Rank for survival	1	2	3	4	5	6	7	8	9
1	Top 20%	0.884	0.895	0.889	0.865	0.834	0.778	0.796	0.829	0.840
	60 to 80%	0.863	0.860	0.859	0.830	0.783	0.736	0.739	0.786	0.805
	40 to 60%	0.832	0.831	0.818	0.789	0.741	0.709	0.696	0.756	0.773
	20 to 40%	0.806	0.809	0.793	0.762	0.706	0.662	0.653	0.718	0.748
	Bottom 20%	0.755	0.749	0.731	0.691	0.644	0.585	0.586	0.663	0.702
2	Top 20%	0.891	0.909	0.901	0.888	0.858	0.827	0.822	0.855	0.855
	60 to 80%	0.873	0.875	0.874	0.868	0.831	0.789	0.783	0.810	0.823
	40 to 60%	0.849	0.861	0.854	0.833	0.791	0.767	0.748	0.785	0.799
	20 to 40%	0.823	0.833	0.831	0.813	0.767	0.730	0.725	0.745	0.770
	Bottom 20%	0.791	0.786	0.782	0.760	0.720	0.667	0.659	0.712	0.727
3	Top 20%	0.902	0.909	0.909	0.901	0.870	0.837	0.828	0.844	0.868
	60 to 80%	0.876	0.889	0.884	0.870	0.843	0.815	0.781	0.831	0.826
	40 to 60%	0.861	0.870	0.862	0.850	0.821	0.774	0.747	0.797	0.815
	20 to 40%	0.834	0.842	0.840	0.825	0.801	0.744	0.731	0.761	0.783
	Bottom 20%	0.785	0.813	0.800	0.791	0.754	0.723	0.690	0.724	0.750
4	Top 20%	0.904	0.907	0.907	0.891	0.862	0.828	0.819	0.842	0.848
	60 to 80%	0.878	0.880	0.879	0.869	0.843	0.817	0.783	0.804	0.820

	40 to 60%	0.863	0.861	0.859	0.848	0.814	0.779	0.754	0.780	0.799
	20 to 40%	0.827	0.836	0.830	0.820	0.792	0.749	0.723	0.745	0.780
	Bottom 20%	0.795	0.797	0.801	0.783	0.747	0.714	0.681	0.729	0.734
5	Top 20%	0.890	0.896	0.885	0.883	0.847	0.831	0.811	0.814	0.842
	60 to 80%	0.870	0.875	0.872	0.855	0.823	0.783	0.767	0.785	0.800
	40 to 60%	0.844	0.850	0.848	0.828	0.801	0.772	0.724	0.780	0.779
	20 to 40%	0.823	0.828	0.821	0.811	0.772	0.733	0.693	0.727	0.764
	Bottom 20%	0.771	0.787	0.787	0.758	0.719	0.679	0.673	0.687	0.703
6	Top 20%	0.890	0.879	0.887	0.863	0.841	0.814	0.796	0.821	0.826
	60 to 80%	0.867	0.865	0.856	0.831	0.802	0.765	0.740	0.777	0.806
	40 to 60%	0.826	0.835	0.830	0.810	0.762	0.728	0.710	0.737	0.777
	20 to 40%	0.799	0.801	0.808	0.786	0.745	0.690	0.676	0.695	0.743
	Bottom 20%	0.780	0.770	0.764	0.743	0.698	0.650	0.638	0.664	0.702
7	Top 20%	0.876	0.878	0.862	0.851	0.823	0.763	0.756	0.790	0.813
	60 to 80%	0.843	0.854	0.845	0.824	0.761	0.726	0.721	0.764	0.764
	40 to 60%	0.835	0.828	0.812	0.789	0.744	0.705	0.684	0.727	0.751
	20 to 40%	0.801	0.778	0.773	0.745	0.714	0.653	0.654	0.712	0.721
	Bottom 20%	0.737	0.741	0.740	0.711	0.659	0.594	0.593	0.601	0.684
8	Top 20%	0.838	0.845	0.837	0.804	0.754	0.687	0.692	0.736	0.771
	60 to 80%	0.806	0.800	0.787	0.756	0.701	0.681	0.657	0.682	0.715
	40 to 60%	0.773	0.768	0.763	0.737	0.671	0.636	0.605	0.638	0.689
	20 to 40%	0.713	0.735	0.714	0.690	0.642	0.569	0.553	0.568	0.650
	Bottom 20%	0.677	0.668	0.689	0.629	0.588	0.539	0.514	0.603	0.634

Supplementary Table S9.10: Fertility transition matrix with probabilities of transitioning from the current state to transition state month of calving groups (MOCG) which are 1 (January), 2 (February), 3 (March), 4 (April), 5 (May), 6 (June), 7 (July and August), 8 (September), 9 (October to December), as well as MOCGs 10 (January), 11 (February and March), and 12 (April to August) which capture a two calendar year lag between successive calvings; probabilities have been stratified based on an animal's rank for calving interval (CIV).

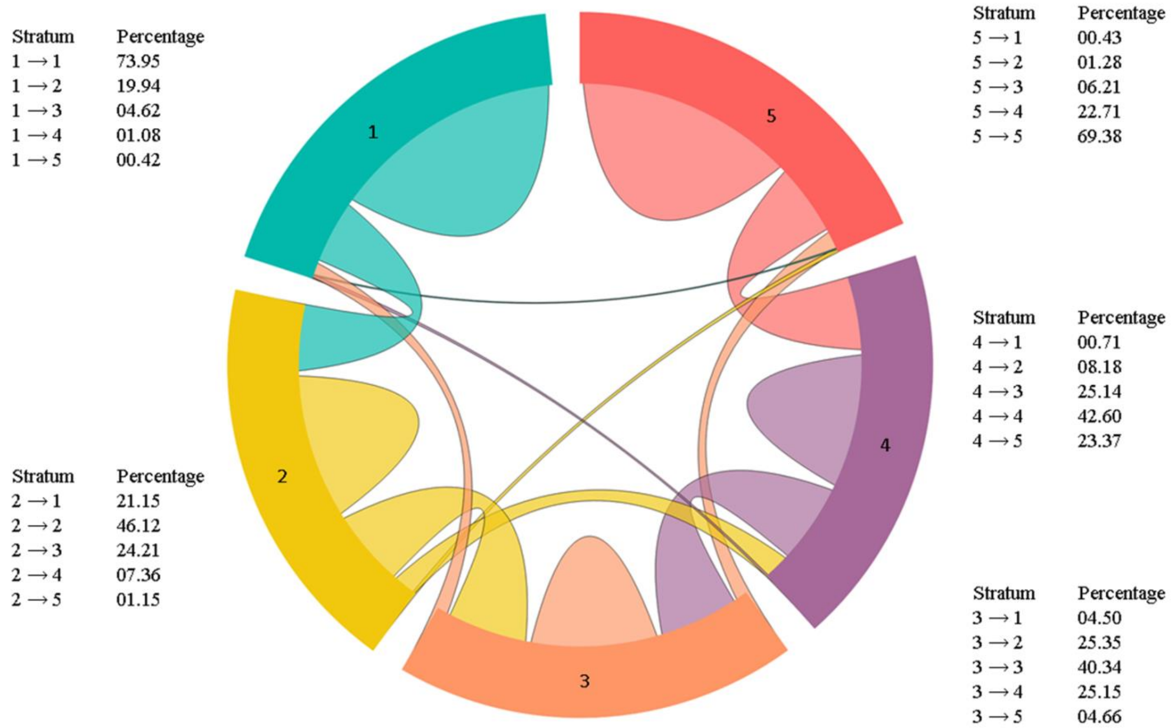
Current state MOCG		Transition state month of calving											
		1	2	3	4	5	6	7	8	9	10	11	12
	Rank for CIV												
1	Top 20%	0.358	0.225	0.145	0.068	0.028	0.010	0.009	0.001	0.156	0.000	0.000	0.000
	60 to 80%	0.349	0.223	0.144	0.075	0.032	0.011	0.010	0.001	0.155	0.000	0.000	0.000
	40 to 60%	0.339	0.225	0.153	0.081	0.031	0.013	0.010	0.001	0.146	0.000	0.000	0.000
	20 to 40%	0.328	0.221	0.165	0.089	0.035	0.015	0.013	0.001	0.132	0.000	0.000	0.000
	Bottom 20%	0.291	0.212	0.177	0.110	0.048	0.020	0.018	0.002	0.122	0.000	0.000	0.000
2	Top 20%	0.158	0.367	0.289	0.106	0.037	0.012	0.008	0.002	0.020	0.000	0.000	0.000
	60 to 80%	0.149	0.358	0.296	0.114	0.038	0.013	0.010	0.004	0.019	0.000	0.000	0.000
	40 to 60%	0.146	0.347	0.292	0.126	0.043	0.013	0.012	0.004	0.018	0.000	0.000	0.000
	20 to 40%	0.137	0.329	0.297	0.140	0.047	0.016	0.013	0.005	0.016	0.000	0.000	0.000

	Bottom 20%	0.126	0.304	0.294	0.150	0.059	0.021	0.021	0.006	0.018	0.000	0.000	0.000
3	Top 20%	0.022	0.190	0.453	0.228	0.068	0.020	0.013	0.003	0.003	0.000	0.000	0.000
	60 to 80%	0.020	0.183	0.451	0.231	0.071	0.022	0.015	0.004	0.004	0.000	0.000	0.000
	40 to 60%	0.019	0.172	0.448	0.239	0.073	0.024	0.017	0.004	0.004	0.000	0.000	0.000
	20 to 40%	0.017	0.163	0.435	0.246	0.082	0.027	0.020	0.005	0.006	0.000	0.000	0.000
	Bottom 20%	0.016	0.147	0.412	0.260	0.093	0.033	0.025	0.008	0.008	0.000	0.000	0.000
4	Top 20%	0.000	0.033	0.302	0.415	0.163	0.047	0.027	0.006	0.007	0.000	0.000	0.000
	60 to 80%	0.000	0.028	0.292	0.420	0.165	0.049	0.031	0.007	0.009	0.000	0.000	0.000
	40 to 60%	0.000	0.028	0.282	0.416	0.169	0.053	0.034	0.007	0.011	0.000	0.000	0.000
	20 to 40%	0.000	0.023	0.271	0.418	0.173	0.054	0.038	0.010	0.013	0.000	0.000	0.000
	Bottom 20%	0.000	0.020	0.244	0.400	0.190	0.064	0.047	0.014	0.021	0.000	0.000	0.000
5	Top 20%	0.000	0.000	0.082	0.367	0.331	0.118	0.069	0.013	0.017	0.002	0.000	0.000
	60 to 80%	0.000	0.000	0.069	0.360	0.336	0.120	0.076	0.014	0.022	0.002	0.000	0.000
	40 to 60%	0.000	0.000	0.067	0.351	0.336	0.122	0.078	0.016	0.026	0.003	0.000	0.000
	20 to 40%	0.000	0.000	0.059	0.337	0.333	0.130	0.088	0.019	0.031	0.004	0.000	0.000
	Bottom 20%	0.000	0.000	0.048	0.307	0.332	0.135	0.098	0.026	0.047	0.006	0.000	0.000

6	Top 20%	0.000	0.000	0.001	0.151	0.377	0.236	0.161	0.027	0.037	0.009	0.002	0.000
	60 to 80%	0.000	0.000	0.000	0.127	0.364	0.251	0.170	0.029	0.044	0.013	0.002	0.000
	40 to 60%	0.000	0.000	0.001	0.110	0.355	0.261	0.171	0.033	0.050	0.016	0.003	0.000
	20 to 40%	0.000	0.000	0.001	0.099	0.337	0.259	0.187	0.037	0.056	0.021	0.004	0.000
	Bottom 20%	0.000	0.000	0.000	0.087	0.305	0.255	0.196	0.044	0.078	0.030	0.005	0.000
7	Top 20%	0.000	0.000	0.000	0.001	0.081	0.205	0.464	0.107	0.094	0.020	0.026	0.003
	60 to 80%	0.000	0.000	0.000	0.001	0.070	0.184	0.466	0.118	0.106	0.023	0.030	0.003
	40 to 60%	0.000	0.000	0.000	0.001	0.059	0.166	0.472	0.122	0.116	0.025	0.036	0.004
	20 to 40%	0.000	0.000	0.000	0.000	0.051	0.151	0.453	0.137	0.128	0.034	0.042	0.003
	Bottom 20%	0.000	0.000	0.000	0.001	0.044	0.131	0.426	0.139	0.154	0.044	0.056	0.006
8	Top 20%	0.000	0.000	0.000	0.000	0.000	0.001	0.304	0.314	0.264	0.034	0.051	0.031
	60 to 80%	0.000	0.000	0.000	0.000	0.000	0.001	0.271	0.325	0.278	0.040	0.056	0.030
	40 to 60%	0.000	0.000	0.000	0.000	0.000	0.000	0.248	0.325	0.290	0.046	0.059	0.032
	20 to 40%	0.000	0.000	0.000	0.000	0.000	0.000	0.225	0.318	0.306	0.048	0.069	0.033
	Bottom 20%	0.000	0.000	0.000	0.000	0.000	0.000	0.195	0.302	0.316	0.060	0.086	0.041
9	Top 20%	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.104	0.516	0.130	0.133	0.091
	60 to 80%	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.094	0.518	0.133	0.140	0.094

40 to 60%	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.094	0.509	0.136	0.148	0.095
20 to 40%	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.091	0.496	0.138	0.154	0.105
Bottom 20%	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.079	0.471	0.139	0.172	0.126

9.3 Supplementary Figures



Stratum	Percentage
1 → 1	73.95
1 → 2	19.94
1 → 3	04.62
1 → 4	01.08
1 → 5	00.42

Stratum	Percentage
5 → 1	00.43
5 → 2	01.28
5 → 3	06.21
5 → 4	22.71
5 → 5	69.38

Stratum	Percentage
4 → 1	00.71
4 → 2	08.18
4 → 3	25.14
4 → 4	42.60
4 → 5	23.37

Stratum	Percentage
2 → 1	21.15
2 → 2	46.12
2 → 3	24.21
2 → 4	07.36
2 → 5	01.15

Stratum	Percentage
3 → 1	04.50
3 → 2	25.35
3 → 3	40.34
3 → 4	25.15
3 → 5	04.66

Supplementary Figure S9.1: Transition probability of milk yield performances into different strata from the initial strata (identified in bordering circular segments).