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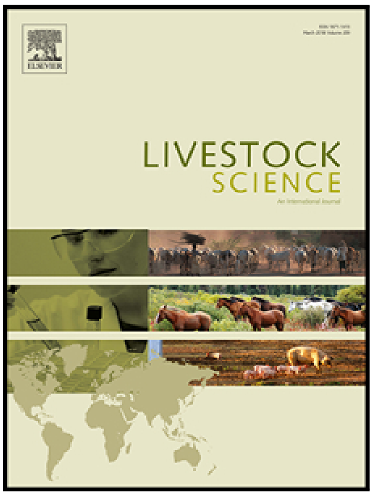

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S.C. Ring , R.D. Evans , M.L. Doherty , D.P. Berry

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HIGHLIGHTS:

- The genetic standard deviation for mortality ranged from 0.005 to 0.034
- Direct heritability estimates for mortality ranged from 0.003 to 0.049 ($P < 0.05$)
- Genetic correlations among mortality in different cow parities were moderate to strongly positive
- Results can inform genetic evaluations for mortality and the genetic gain achievable

Genetic parameters for animal mortality in pasture-based, seasonal-calving dairy and beef herds

S. C. Ring[a, b], R. D. Evans[c], M. L. Doherty[b], and D. P. Berry[a*]

[a] Teagasc, Animal and Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland

[b] School of Veterinary Medicine, University College Dublin, Belfield, Dublin 4, Ireland

[c] Irish Cattle Breeding Federation, Highfield House, Bandon, Co. Cork, Ireland

[*] Corresponding Author: donagh.berry@teagasc.ie

ABSTRACT

In the absence of informative health and welfare phenotypes, breeding for reduced animal mortality could improve overall health and welfare, provided genetic variability in animal mortality exists. The objective of the present study was to estimate genetic (and other) variance components for animal mortality in pasture-based, seasonal-calving dairy and beef herds across multiple life stages as well as to quantify the genetic relationship in mortality among life stages. National mortality records were available for all cattle born in the Republic of Ireland. Cattle were grouped into three life stages based on age (0 to 30 days, 31 to 365 days, 366 to 1095 days) whereas females with ≥ 1 calving event were also grouped into five life stages, based on parity number (1, 2, 3, 4, and 5), considering both the initial 60 days of lactation and a cow's entire lactation period, separately. The mean mortality prevalence ranged from 0.70 to 5.79% in young animals and from 0.53 to 3.86% in cows. Variance components and genetic correlations were estimated using linear mixed models using 21,637 to 100,993 records. Where heritability estimates were different from zero, direct heritability estimates for mortality in young animals (≤ 1095 days) ranged from 0.006 to 0.040, whereas the genetic standard deviation ranged from 0.015 to 0.034. The contribution of a maternal genetic effect to mortality in young animals was evident up to 30 days of age in dairy herds, but this was only the case in preliminary analysis of stillbirths in beef herds. Based on the estimated genetic standard deviation in the present study, the incidence of mortality in young animals could be reduced through breeding by up to 3.4 percentage units per generation. For cows, direct heritability estimates for mortality, where different from zero, ranged from 0.003 to 0.049. The genetic standard deviation for mortality in cows ranged from 0.005 to 0.016 during the initial 60 days of lactation and ranged from 0.011 to 0.032 during the cow's entire lactation. Genetic correlations among the age groups as well as between the age groups and cow parities had high standard errors. Genetic correlations among the cow parities were moderate to strongly positive (ranging from 0.66 to 0.99) and mostly different from zero. Results from the present study can be used to inform genetic evaluations for mortality in young animals and in cows as well as the potential genetic gain achievable.

Key words: beef, cow mortality, dairy, death, genetics, young animal mortality.

INTRODUCTION

Animals with compromised health status have reduced productivity (Stott et al., 2012) and shorter longevity (Smith, 1998; Bar et al., 2008) as well as contributing to greater intensity of greenhouse gas emissions (Gerber et al., 2013). Breeding for healthier animals is an inexpensive method to improve animal health, welfare and production, yet breeding strategies for improved animal health are often limited by the lack of accurate phenotypes (Berry et al., 2011). Since all Irish cattle producers must declare each on-farm death on the Irish Bovine Animal Identification System (Statutory Instrument No. 655/2003), a vast quantity of mortality phenotypes are routinely available (at no cost) to generate genetic evaluations for animal mortality. However, genetic parameters must first be quantified.

Despite differing causes of mortality at varying life stages (AFBI and DAFM, 2016), existing genetic parameter estimates for mortality in beef herds are entirely limited to the period from birth to weaning (Goyache et al., 2003; Eriksson et al., 2004; Riley et al., 2004); moreover, they are estimated from relatively small datasets for a limited number of beef breeds. With the exception of one study which considered only females (Fuerst-Waltl and Fuerst, 2010), genetic parameters for mortality in nulliparous dairy animals have been restricted to the period from birth to 180 days of age. There are only three studies (Miller et al., 2008; Maia et al., 2014; VanRaden et al., 2016) on genetic parameters for mortality in cows and these were limited to dairy populations. With the exception of stillbirths (Pryce et al., 2006), to our knowledge, there are no estimates of genetic parameters for mortality in seasonal-calving production systems, in either dairy or beef herds. Furthermore, genetic correlations between mortality at different life stages are limited to just a few life stages (Goyache et al., 2003; Hansen et al., 2003; Norberg et al., 2013). There is therefore a paucity of information pertaining to mortality in cattle, especially older cattle, and more so in beef cattle.

Therefore, the objective of the present study was to quantify the genetic variance components for animal mortality across relevant periods of an animal's lifetime in pasture-based, seasonal-calving dairy and beef herds. Genetic correlations for mortality between life stages will also be estimated. Results will be useful to determine the feasibility and expected rate of genetic gain of including mortality traits in national breeding objectives.

MATERIALS AND METHODS

Irish cattle producers are legally required to inform the Department of Agriculture, Food and the Marine (http://www.agriculture.gov.ie) of the date, the source, and destination location as well as the unique animal identification number for each animal birth, calving, farm transfer, and animal death. These data, together with individual animal calving performance, artificial insemination and natural service measures, were extracted on the 31st of December 2015 from the Irish Cattle Breeding Federation database (ICBF; http://www.icbf.com). Data consisted of 8,046,228 males and females born between the years 2009 and 2012, inclusive as well as 2,102,916 cows (i.e., females with ≥ 1 calving event) born after the 1st of January 2005 that calved for the first time between the years 2007 and 2012, inclusive.

Within-herd management protocols were not available to the present study. That said, Irish calves in beef herds tend to be reared by their dams at pasture up to approximately 9 months of age (weaning); thereafter, weaned cattle are then typically either sold to producers intending to grow cattle for slaughter or they are retained by the original producer and managed with other cattle of a similar age. In contrast, calves born in Irish dairy herds are artificially reared on either whole-milk or milk-replacer from birth until approximately 8 weeks of age (weaning); after weaning calves remaining in dairy herds tend to be managed as a uniform group at pasture. Cows of the same parity that calve in close proximity to each other tend to be managed uniformly both within dairy herds and beef herds.

Definition of mortality

As previously described by Ring et al. (2018) in their analysis of mortality in Irish cattle, each animal's lifetime was stratified into seven categories in the present study, based on animal age, and where relevant, five categories based on parity number. Briefly, the animal age groups were 0 to 2 days, 3 to 7 days, 8 to 30 days, 31 to 182 days, 183 to 365 days, 366 to 730 days, and 731 to 1,095 days. Preliminary analyses of the seven age groups revealed that the direct and maternal heritability estimates in both dairy and beef herds were both very low (i.e., direct heritability estimates ≤ 0.04) and mostly not different from zero ($P > 0.05$; Table 1). Therefore, the seven age groups were collapsed to three age groups, namely 0 to 30 days, 31 to 365 days, and 366 to 1095 days. Cow parities included first through to fifth parity inclusive, where parity signified a cow's parity number the day after calving. Mortality was defined as a binary trait within each age group and cow parity separately. For each age group, animals that died during that age group were defined as dead (1), whereas animals that survived the entire duration of that age group were defined as alive (0); mortality per age group was only considered for animals that had the full opportunity to express their phenotype (e.g., animals younger than the specified age or previously defined as dead were not considered).

Mortality in cows was defined in two ways. The first definition considered a cow's entire lactation period whereas the second definition considered only the initial 60-day post-partum period. When considering cow mortality for the entire lactation, cows that died prior to reaching parity *i+1* were assumed to have died (1) in parity *i*, while cows that reached parity *i +1* were assumed to have survived (0) parity *i;* only cows alive at the beginning of parity *i* were considered for inclusion in the definition of mortality for parity *i*. For cow mortality in the early post-partum period, cows that died in the initial 60 days post-partum period were defined as dead (1) while cows that survived > 60 days post-partum were defined as alive (0). Mortality traits per cow parity *i* were only considered if the cow reached parity *i +1* or if the cow died during parity *i*; therefore, cows that were slaughtered or exported did not have a phenotype for parity *i*.

Data edits

Cows that calved ≤ 545 days of age (15,019 cows) were discarded, as were the 83,904 calving events resulting in > 2 progeny. Furthermore, animals born to dams that were either ≤ 545 days of age (307 animals) or ≥ 4,380 days of age (19,683 animals) were removed. A total of 32,079 cows that calved ≥ 545 days from the parity median were removed as were 162 cows that calved for the first time ≥ 1380 days of age. Pedigree information for each animal was traced back to founders and founder animals were assigned a genetic group based on breed. A total of 189,159 animals without a known sire were discarded. When the variable of interest was mortality in young animals (i.e., ≤ 1095 days), then only records from animals also with a known maternal grand-sire were retained; a further 152,450 animals were discarded. Heterosis and recombination loss coefficients for each animal were calculated as:

$1-\sum_{i=1}^{n} sire_i \cdot dam_i$ and $1-\sum_{i=1}^{n} \frac{sire_i^2 + dam_i^2}{2}$, respectively where $sire_i$ and dam_i were the proportion of breed *i* in the sire and dam, respectively (VanRaden and Sanders, 2003). Animals that did not reside in the same herd for mortality age group *i* and *i+1* were not considered for age group *i+1*. Cows that did not calve in the same herd for parity *i* and parity *i +1* were removed from the analysis for parity *i.* Following these edits, 21,148,754 records from 9,489,538 animals remained.

Herd-years that did not have at least one calving were removed as were herds that were not defined as either a beef or a dairy herd-type; the average breed proportion of calved cows in a herd-year was used to determine if the herd-type was either beef or dairy as per Ring et al. (2018). Where the average breed proportion of calved cows in a herd-year was ≤ 55% of a dairy breed (i.e., Ayrshire, Brown Swiss, Friesian, Holstein, Jersey, Montbéliarde, Norwegian Red, Normande) the herd-type was defined as a beef herd. Where the average breed proportion of calved cows in a herd-year was ≥ 85% a dairy breed, the herd-type was defined as a dairy herd. To represent seasonal-calving herds which predominate in Ireland, only mortality records from herds that calved at least 70% of cows between the months January to June, inclusive were considered. Additionally, only herds that recorded at least one animal death within a given mortality age category from the 1st January 2005 to 31st December 2015, inclusive, were considered for the analysis of that mortality age category; this edit was not imposed on cow parities due to a scarcity of phenotypes.

Animals were assigned a contemporary group for each age and parity category separately, using the methods adapted from Crump et al. (1997) and Berry et al. (2013). Formation of contemporary groups involved clustering animals within a herd that were either born or calved within 10 days of each other; where < 10 animals were initially clustered together, these animals were amalgamated with an adjacent group of animals, until a group contained at least 10 animals, provided that the number of days between the first and final event did not exceed 90 days. For each age group, an animal was assigned a contemporary group based on their birth date and the herd they resided in during each respective age group. For cow mortality traits, cows were assigned a contemporary group for each cow-parity separately, based on their date of calving and herd at calving. For each of the age groups, contemporary groups with < 5 animals were removed, whereas for cow parities, contemporary groups with < 4 animals were removed. Following selection of a random sample of contemporary groups, the dataset included approximately 100,000 mortality phenotypes per mortality category; in beef herds, < 32,000 records remained for third and greater parity cows, and therefore they were not considered in statistical analyses except for the repeatability model that considered all cow parities (i.e., parity 1, 2, 3, 4, and 5) in the same analysis. The number of records in the final analyses per age group and per parity is in Table 2 and Table 3, respectively. The percentage of animals sired by an artificial insemination sire ranged from 68 to 96% for the dairy herd analyses and from 20 to 27% for the beef herd analyses. The percentage of sires that had progeny in >1 contemporary group ranged from 30 to 46% for the dairy herd analyses and from 18 to 30% for the beef herd analyses.

Statistical analyses

Genetic parameters for mortality were estimated using linear mixed models in ASReml (Gilmour et al., 2009) for each age and parity category separately; dairy and beef herds were analyzed separately. The fitted linear models were:

$$\begin{aligned} young\ animals &= cg + het_a + rec_a + het_d + rec_d + sex_a + twin_a + age_d \\ &+ parity_d + a + d + pe_d + e \end{aligned}$$

$$cows = cg + het_a + rec_a + twin_a + age_d + parity_d + age_a + sex_p + twin_p + a + e$$

Where *young animals* = the dependent mortality variable of age group; *cows* = the dependent mortality variable for cows; *cg* is the fixed effect of contemporary group; subscripts *a*, *d* and *p* = the animal, the animal's dam, and the animal's progeny, respectively; *het* = the fixed effect of heterosis coefficient (0.00, 0.01 to 0.09, 0.10 to 0.19, 0.20 to 0.29 … 0.90 to 0.99, 1.00), *rec* = the fixed effect of recombination loss coefficient (0.00 to 0.09, 0.10 to 0.29, 0.30 to 0.49 and ≥ 0.50); *sex* = the fixed effect of the gender (considered only for singleton births in the cow analyses); *twin* = the fixed effect of single or twin births; *age* = the fixed effect of age at calving relative to the parity by herd-type median; *parity* = the fixed effect of parity (1, 2, 3, 4, 5, >5) at the animal's birth; *a* = the random effect of the direct additive genetic component, where $a \sim N(0, \mathbf{A}\sigma^2_a)$ with σ^2_a representing the additive genetic variance of the animal and **A** the additive genetic relationship matrix among animals; *d* is the random effect of the maternal additive genetic component, where $d \sim N(0, \mathbf{A}\sigma^2_d)$ with σ^2_d representing the additive genetic variance of the animal's dam and **A** the additive genetic relationship matrix among animals; pe_d = the random effect of permanent environment of the animal's dam, where $pe_d \sim N(0, \mathbf{I}\sigma^2_{ped})$ with σ^2_{ped} representing the permanent environmental variance of the animal's dam and **I** an identity matrix; *e* = the random residual effect, where $e \sim N(0, \mathbf{I}\sigma^2_e)$ with σ^2_e representing the residual variance and **I** an identity matrix.

In addition, using repeatability linear mixed models in ASReml (Gilmour et al., 2009), genetic parameters for mortality of young animals were estimated when each age group were considered in the same analysis to account for multiple observations per animal in the one analysis; similarly genetic parameters for mortality in cows were estimated using a repeatability model when each cow parity were considered in the same analysis to account for multiple observations per cow in the one analysis. In all analyses, dairy and beef herds were analyzed separately. When repeatability models were used, the random effect of the permanent environment of the animal was considered in analyses as was the fixed effect of mortality group (i.e., age group or parity) together with all other fixed and random effects that were included in the linear models.

Genetic correlations among mortality at different life stages were estimated using ASReml (Gilmour et al., 2009); the models fitted were the same as the linear models except for the additive genetic components where the animal's sire was the additive genetic component in the cow parity analyses whereas both the animal's sire and the animal's maternal-grandsire were the additive genetic components in the age group analyses. For the bivariate analyses of mortality among the age groups, the genetic correlation between the direct and maternal effects within age group were constrained to zero. The coefficient of genetic variation (CV) was calculated for each trait using methods described by Burdon (2008) to adjust for the binary nature of the traits.

RESULTS

Genetic parameters for mortality in young animals

With the exception of mortality > 30 days of age in beef herds, where no heritability was evident or the standard error was large, direct heritability estimates for mortality in dairy and beef herds when each of the three age cohorts were analyzed separately were different from zero ($P < 0.05$) and ranged from 0.006 to 0.019 (Table 2). The coefficient of direct genetic variation for mortality in young animals ranged from 8% to 20% in dairy herds and from 1% to 14% in beef herds (Table 2). The contribution of a maternal genetic effect to mortality in young animals was only detected for calves aged 0 to 30 days in dairy herds, but only in preliminary analysis of stillbirths in beef herds (Table 2). When mortality was restricted to the first two days of life, only considered in the preliminary analysis, the contribution of a maternal genetic effect was observed in beef herds (i.e., maternal heritability = 0.01; $P < 0.05$; Table 1), but not in dairy herds. The presence of a maternal permanent environmental variance up to 365 days of age in dairy herds and up to 30 days of age in beef herds suggests some repeatability in the dam for producing progeny that die (Table 2); where a maternal permanent environmental variance effect was detected ($P < 0.05$) in either dairy or beef herds, the effect accounted for a larger proportion of the phenotypic variability in mortality than the direct genetic or the maternal genetic effect. For example, maternal permanent environmental variance accounted for 3% to 20% of the phenotypic variation in mortality up to 365 days of age in dairy herds and 6% of the phenotypic variation in mortality between 0 to 30 days of age in beef herds.

When a repeatability model was used to analyze each of the three age cohorts together (i.e., multiple observations per animals), the direct heritability estimate for mortality in young animals was 0.03 (SE = 0.005) in dairy herds and 0.04 (SE = 0.008) in beef herds; in both analyses the corresponding direct genetic standard deviation was 0.034. A maternal genetic effect was different from zero using the repeatability model in dairy herds (i.e., maternal heritability = 0.005; SE = 0.002) but not in beef herds.

Genetic parameters for cow mortality

When each cow parity was analyzed separately, the direct heritability estimates for mortality both during the initial 60 days of lactation and during a cow’s entire lactation (Table 3), where different from zero, ranged from 0.003 to 0.049. The coefficient of genetic variation for cow mortality ranged from 3% to 11% in dairy herds and from 7% to 22% in beef herds (Table 3). When the repeatability model was used, which combined the five cow parities in the same analysis, heritability estimates ranged from 0.002 (SE = 0.001; first 60 days post-partum) to 0.006 (SE = 0.002; entire cow lactation) in dairy herds and from 0.008

(SE = 0.005; first 60 days post-partum) to 0.011 (SE = 0.005; entire cow lactation) in beef herds.

Genetic correlations for mortality across life stages

Genetic correlations for mortality across the age groups in both dairy and beef herds were mostly not different from zero ($P > 0.05$; i.e., SE were large relative to the estimates) and the sign of the correlations was not consistent (Table 4). In both dairy and beef herds, the genetic correlations for mortality between the age groups and cow parities were mostly not different from zero (Table 4); however, there was a general tendency for family lines that were more susceptible to die ≤ 1095 days of age to also be genetically predisposed to death as cows. In dairy herds, the genetic correlations for mortality in different cow parities were all moderately to strongly positive and different from zero ($P < 0.05$), when the entire duration of lactation was considered (i.e., correlations ranged from 0.66 to 0.99; Table 5). Standard errors of the genetic correlations across parities tended to be larger when mortality was restricted to just 60 days postpartum in dairy herds, yet the general direction of the genetic correlations among cow parities were still moderately to strongly positive (Table 5). In beef herds, the genetic correlation for cow mortality between first and second parity when the entire lactation was considered was 0.99 (SE = 0.129) but not different from zero (i.e., -0.41; SE = 0.289) when mortality was restricted to just the first 60 days of lactation.

DISCUSSION

Genetic selection for reduced animal mortality has the potential to improve animal health and welfare standards, as long as it can be shown that exploitable genetic variation for mortality exists. Relatively few studies have quantified the genetic parameters for animal mortality in dairy herds (Hansen et al., 2003; Miller et al., 2008; Fuerst-Waltl and Sørensen, 2010; Norberg et al., 2013; Maia et al., 2014; VanRaden et al., 2016), and even fewer in beef herds (Goyache et al., 2003; Eriksson et al., 2004; Riley et al., 2004). Furthermore, to our knowledge, no study has quantified genetic parameters for mortality in pasture-based, seasonal-calving systems across many life stages in both dairy and beef cattle herds.

Genetic parameters for mortality in dairy herds

Both the direct and maternal heritability estimates for mortality in young animals in the present study were low, yet comparable to other studies on dairy cattle that also used linear models. Previous direct heritability estimates for mortality of young dairy cattle (i.e., 1 day of age up to the day before calving) ranged from 0.001 to 0.042 (Hansen et al., 2003; Fuerst-Waltl and Sørensen, 2010; Norberg et al., 2013) while previous maternal heritability estimates were < 0.0015 and not always different from zero (Hansen et al., 2003; Norberg et al., 2013).

To our knowledge, there are only three studies on the genetic parameters for cow mortality in dairy herds (Miller et al., 2008; Maia et al., 2014; VanRaden et al., 2016). Miller et al. (2008) reported a heritability estimate ($P < 0.05$) of 0.013 in US dairy cows, whereas Maia et al. (2014) documented heritability estimates ($P < 0.05$) of 0.024, 0.019 and 0.054 for Holstein, Jersey and Danish Red cows, respectively; both studies (Miller et al., 2008; Maia et al., 2014) only defined mortality as death during the entire lactation and they used only a repeatability model to consider all cow parities in the same analysis.

Genetic parameters for mortality in beef herds

To our knowledge, there are no estimates of the genetic parameters for cow mortality in beef cows while there are few such studies (Goyache et al., 2003; Eriksson et al., 2004; Riley et al., 2004) in young beef animals. In contrast to the present study, others (Goyache et al., 2003; Riley et al., 2004) reported a higher direct and maternal heritability estimate on the observable scale for young animal mortality in beef herds up to weaning. Nevertheless, those studies reported a higher incidence of mortality, they were based on confinement systems, they considered only two breeds between them, and they were restricted to small datasets. For example, using 36,125 records from the Spanish Asturiana de los Valles beef breed, Goyache et al. (2003) estimated direct and maternal heritability estimates for mortality using linear models for three periods up to weaning of 0.084 to 0.142 and 0.031 to 0.050, respectively; maternal permanent environmental variance accounted for 1.1% to 1.9% of the observed variation in young animal mortality; standard errors were, however, not reported in that study while the mortality incidence for the three periods ranged from 3.7% to 8.6%. Riley et al. (2004) reported direct and maternal heritability estimates for pre-weaning mortality (i.e., from birth to approximately 7 months) of 0.06 (SE = 0.05) and 0.09 (SE = 0.04), respectively, in purebred and crossbred US Brahman beef calves; in that linear model, a maternal permanent environmental variance was not statistically significant and thus it was excluded from the final model. The study by Riley et al. (2004) reported a higher incidence (11%) of mortality than the present study, it was restricted to data from just one herd over a 47-year period, and contained only 3,552 records in the analysis. To compare heritability estimates for mortality in the present study with the studies by Goyache et al. (2003) and Riley et al. (2004), the observed binary-scale heritability estimates and the reported incidence of the respective datasets, were transformed to the underlying liability scale using the methods outlined by Robertson and Lerner (1949). When the respective heritability estimates for mortality prior to weaning were transformed to the underlying scale, our estimate on the underlying liability scale (0.23) that considered all age groups together (i.e., used in the repeatability model) was within the range of both Riley et al. (2004; 0.17) and Goyache et al. (2003; 0.47). Contrary to the aforementioned US and Spanish studies, a Swedish study

(Eriksson et al., 2004) reported direct and maternal heritability estimates for stillborn calves (i.e., ≤ 24 hours after birth) born to first parity and later parity Charolais and Hereford cows using linear models that were more similar to the present study. Direct heritability estimates ranged from 0.002 to 0.004 in calves born to first parity cows and from 0.006 to 0.010 in calves born to later parity cows, while maternal heritability estimates ranged from 0.001 to 0.005 and maternal permanent environmental variance accounted for < 2% of the total observed variation in stillbirths; however, that study also reported no standard errors for the ratio statistics and they considered just 7,571 to 29,506 records per analysis.

Reasons for low heritability and achieving genetic gain

The low heritability estimates for mortality in the present study (and elsewhere) were expected due to the complexity of causes of premature mortality in cattle (Thomsen et al., 2004; AFBI and DAFM, 2016) ranging from death due to viral, bacterial, or a pathogenic infection or even secondary illnesses arising from earlier infections. Moreover, it is likely that in some cases (albeit a few) accidents may have resulted in premature cattle mortality. The complexity of reasons for animal death likely contributed to the large residual variation and subsequently low heritability estimates observed in the present study, both for young animals and for cows. In addition, although inaccurate mortality recording is unlikely to have reduced heritability estimates in the present study, as Irish producers are legally required to record births and deaths, inaccurate parentage recording may have deflated the heritability estimates. Assuming sires were incorrectly recorded for 13.28% (Purfield et al., 2016) of animals in the present study, the true direct heritability estimates for mortality likely ranges from 0.008 to 0.053 in young animals (Van Vleck, 1970) and from 0.003 to 0.065 in cows.

The annual rate of genetic change for a trait is a function of the genetic variance, the accuracy of selection, the intensity of selection, and the generation interval. The heritability statistic only influences the accuracy of selection; yet when data are abundantly and routinely available, with recorded ancestry, as is the case in Ireland and other countries where notification of all animal birth and deaths is mandatory, the same accuracy of selection can be achieved for low heritability traits as for high heritability traits (Berry et al., 2011). For example, an accuracy of 65% can be achieved for mortality where 75 (assuming a direct heritability of 0.04) to 450 (assuming a direct heritability of 0.0063) half-sib progeny records are available. Therefore, it is likely that genetic variance, not heritability, could limit the extent of genetic gain achievable in Ireland and other EU countries at least. Results from the present study suggest that, based on the genetic standard deviation, the incidence of mortality in both dairy and beef herds could be reduced by up to 3.4 percentage units per generation (or 0.73 percentage units per annum; Schaeffer, 2006) for young animals and up to 3.2 percentage units per generation (or 0.69 percentage units per annum; Schaeffer, 2006) for cows in a single trait selection index, assuming an index reliability of 99%. Considering the genetic standard deviation reported in other studies, the rate of genetic gain achievable for young animals in the present study is similar to that achievable in Danish Holstein (Fuerst-Waltl and Sørensen, 2010) and Danish Jersey (Norberg et al., 2013) calves but lower than that of the Asturiana de los Valles breed up to weaning (Goyache et al., 2003). Nevertheless, results from the present study substantiate that considerable exploitable genetic variation for mortality exists in both dairy and beef cattle.

Genetic correlations for mortality across life stages

A strong positive genetic correlation for mortality between age groups that were close together was expected in the present study (e.g., between 0 to 30 days and 31 to 365 days), while the genetic correlation for mortality between distant age groups (e.g., between 0 to 30 days and 366 to 1095 days) was expected to be weaker; nonetheless, standard errors in the present study were too large to make any strong inferences on the genetic relationship of mortality among ages. Other studies have quantified strong genetic correlations for mortality among young animal age groups (Goyache et al., 2003; Hansen et al., 2003; Norberg et al., 2013). For example, Goyache et al. (2003) reported a direct genetic correlation of 0.75 between perinatal mortality (i.e., ≤ 72 hours) and mortality between 72 hours and weaning in 36,125 Asturiana de los Valles beef calves; however, standard errors were not presented with those estimates. Hansen et al. (2003) documented direct genetic correlations for mortality in dairy herds between 1 days to 14 days of age and 15 days to 60 days of age of 0.73 (SE = 0.10), between 15 days to 60 days of age and 61 days to 180 days of age of 0.54 (SE = 0.13), and between 0 days to 14 days of age and 61 days to 180 days of age of 0.34 (SE = 0.12).

Although the associated standard errors were large, to our knowledge, the present study is the first to quantify both the genetic correlation for mortality between different cow parities as well as between mortality in young animals and cows. Results from the present study suggest that selection for reduced young animal mortality after 30 days of age may be beneficial in reducing cow mortality, and vice versa. That said, selection of reduced mortality during the first month of life may not be beneficial in reducing mortality in later life. Moreover, since the genetic correlations between the cow parities were moderately to strongly positive, albeit not always different from zero, national genetic evaluations for animal mortality could consider using repeatability models which consider all cow parities in the same analysis.

CONCLUSION

Death is a definitive eventual fate arising from compromised health and welfare status. Where data pertaining to specific health and welfare traits are lacking, animal mortality phenotypes can be used to infer health and welfare status by breeding for reduced animal mortality, provided that is, genetic variability exists for animal mortality. Results from the present study suggest that while heritability estimates for animal mortality are (as expected) low, considerable exploitable genetic variability exists. Considerable genetic gain could be achieved, particularly where accurate mortality phenotypes are routinely available at a national level. The extent of genetic gain achievable differed, however, both by life stage and herd-type. Results from the present study also suggest that at least for dairy cows, the genetic expression influencing mortality in primiparae are similar to those affecting mortality in later parities. Animal breeders can use results from the present study to inform genetic evaluations for mortality.

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The authors declare they have no conflict of interest

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Table 1. Number of animals analyzed, the number of dams the animals were born to, the mean mortality prevalence (%), genetic standard deviation for the direct effects ($\sigma_{g\ direct}$), genetic standard deviation for the maternal effects ($\sigma_{g\ maternal}$), the standard deviation for maternal permanent environmental effects ($\sigma_{PE\ maternal}$), the phenotypic standard deviation (σ_p), direct heritability estimates ($h^2_{\ direct}$; SE in parentheses), and maternal heritability estimates ($h^2_{\ maternal}$; SE in parentheses), per age group in dairy and beef herds

Animal age, days	animals	dams	%	$\sigma_{g\ direct}$	$\sigma_{g\ maternal}$	$\sigma_{PE\ maternal}$	σ_p	$h^2_{\ direct}$	$h^2_{\ maternal}$
Dairy herds									
0 to 2	100,993	87,170	1.55	zero	0.0091	0.0466	0.1224	zero	0.0056 (0.0021)
3 to 7	100,386	85,854	0.70	0.0021	0.0056	0.0128	0.0829	0.0007 (0.0011)	0.0046 (0.0018)
8 to 30	100,212	86,610	1.35	0.0065	zero	< 0.0001	0.1135	0.0033 (0.0020)	zero
31 to 182	100,643	86,307	2.44	0.0074	0.0041	< 0.0001	0.1511	0.0024 (0.0017)	0.0007 (0.0009)
183 to 365	100,862	84,866	0.94	0.0024	0.0029	< 0.0001	0.0954	0.0006 (0.0011)	0.0009 (0.0010)
366 to 730	100,409	85,825	1.13	0.0001	0.0007	0.0166	0.1043	zero	zero
731 to 1095	100,667	86,538	1.92	0.0082	0.0026	0.0154	0.1361	0.0036 (0.0018)	0.0004 (0.0009)
Beef herds									
0 to 2	100,399	79,514	1.77	0.0224	0.0124	0.0402	0.1303	0.0295 (0.0080)	0.0090 (0.0039)
3 to 7	100,523	72,919	0.84	0.0099	0.0036	0.0149	0.0903	0.0121 (0.0058)	0.0016 (0.0025)
8 to 30	100,176	78,356	1.21	0.0154	0.0032	0.0164	0.1084	0.0201 (0.0076)	0.0009 (0.0022)
31 to 182	100,340	81,168	1.76	0.0128	0.0066	0.0194	0.1300	0.0096 (0.0057)	0.0026 (0.0026)
183 to 365	100,419	82,356	1.47	0.0245	0.0149	0.0122	0.1176	0.0434 (0.0348)	0.0161 (0.0070)
366 to 730	100,811	90,985	1.70	0.0226	0.0127	0.1282	0.1282	0.0310 (0.0103)	0.0099 (0.0077)
731 to 1095	61,927	55,469	2.93	0.0309	0.0329	0.0135	0.1670	0.0342 (0.0130)	0.0387 (0.0166)

Table 2. Number of animals analyzed, the number of dams the animals were born to, the mean mortality prevalence (%), genetic standard deviation for direct effects ($\sigma_{g\ direct}$), genetic standard deviation for maternal effects ($\sigma_{g\ maternal}$), the standard deviation for maternal permanent environmental effects ($\sigma_{PE\ maternal}$), the phenotypic standard deviation (σ_p), direct heritability estimates (h^2_{direct}; SE in parentheses), and maternal heritability estimates ($h^2_{maternal}$; SE in parentheses), per age group in dairy and beef herds

Animal age, days	animals	dams	%	$\sigma_{g\ direct}$	$\sigma_{g\ maternal}$	$\sigma_{PE\ maternal}$	σ_p	h^2_{direct}	$h^2_{maternal}$
Dairy herds									
0 to 30	100,263	93,713	2.00	0.028	0.015	0.0955	0.2132	0.0168 (0.0043)	0.0047 (0.0020)
31 to 365	100,926	94,323	3.89	0.015	zero	0.0299	0.1870	0.0063 (0.0025)	zero
366 to 1095	100,424	93,561	3.69	0.017	0.006	0.0162	0.1833	0.0091 (0.0029)	0.0009 (0.0013)
Beef herds									
0 to 30	100,737	82,169	3.77	0.026	zero	0.0447	0.1864	0.0192 (0.0060)	zero
31 to 365	100,560	81,476	2.93	0.003	zero	0.0122	0.1651	0.0004 (0.0026)	zero
366 to 1095	21,637	18,735	5.79	0.039	0.015	0.0001	0.2182	0.0319 (0.0186)	0.0047 (0.0103)

Table 3. Number of cows, mean mortality prevalence (%), genetic standard deviation (σ_g), the phenotypic standard deviation (σ_p), and heritability estimates (h^2; SE in parentheses) for cow mortality in both dairy and beef herds per cow parity for both the initial 60 days of lactation and the entire duration of the lactation

		Initial 60 days of lactation				Entire duration of lactation			
Cow parity	cows	%	σ_g	σ_p	h^2	%	σ_g	σ_p	h^2
Dairy herds									
Parity 1	100,902	0.81	0.002	0.089	0.001 (0.0011)	2.56	0.011	0.156	0.005 (0.0021)
Parity 2	100,677	0.71	0.005	0.083	0.004 (0.0015)	2.05	0.011	0.141	0.006 (0.0019)
Parity 3	100,857	0.85	0.005	0.092	0.003 (0.0015)	2.25	0.012	0.148	0.006 (0.0021)
Parity 4	100,550	1.25	0.006	0.110	0.003 (0.0017)	3.11	0.016	0.172	0.009 (0.0028)
Parity 5	82,792	1.62	0.012	0.125	0.009 (0.0033)	3.86	0.020	0.190	0.011 (0.0037)
Beef herds									
Parity 1	62,662	0.65	0.016	0.076	0.043 (0.0110)	2.19	0.032	0.145	0.049 (0.0130)
Parity 2	44,492	0.53	0.008	0.072	0.013 (0.0114)	1.81	0.009	0.132	0.004 (0.0104)

Table 4. Genetic correlations for mortality (SE in parentheses) between the age groups as well as between the age groups and the entire duration of a cow's lactation for each cow parity in dairy and beef herds

	Dairy			Beef		
Category	0 to 30, days	31 to 365, days	366 to 1095, days	0 to 30, days	31 to 365, days	366 to 1095, days
Animal age						
31 to 365, days	-0.04 (0.235)			0.80 (0.564)		
366 to 1095, days	0.45 (0.167)	0.48 (0.232)		-0.42 (0.225)	0.79 (1.275)	
Cow parity						

Parity 1	-0.55 (0.198)	0.93 (0.218)	0.93 (0.153)	0.56 (0.214)	0.76 (1.652)	0.61 (0.246)
Parity 2	0.07 (0.248)	0.00 (0.000)	0.34 (0.287)	-0.81 (0.166)	-0.12 (0.916)	0.18 (0.309)
Parity 3	-0.31 (0.209)	0.24 (0.319)	0.67 (0.255)	-	-	-
Parity 4	-0.27 (0.222)	0.37 (0.293)	0.88 (0.201)	-	-	-
Parity 5	-0.52 (0.202)	0.00 (0.000)	0.30 (0.335)	-	-	-

Table 5. Genetic correlations for mortality (SE in parentheses) between cow parity categories in dairy herds for both the entire duration of a cow's lactation (below the diagonal) and during the initial 60 days of lactation (above the diagonal)

Cow parity	Parity 1	Parity 2	Parity 3	Parity 4	Parity 5
Parity 1		0.79 (0.453)	0.35 (0.511)	0.92 (0.497)	0.80 (0.491)
Parity 2	0.76 (0.214)		0.83 (0.312)	0.88 (0.208)	0.93 (0.233)
Parity 3	0.74 (0.177)	0.98 (0.114)		0.86 (0.251)	0.97 (0.151)
Parity 4	0.66 (0.188)	0.86 (0.172)	0.99 (0.067)		0.07 (0.338)
Parity 5	0.67 (0.166)	0.51 (0.236)	0.98 (0.058)	0.98 (0.133)	