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Contribution of genetic variability to phenotypic differences in on-farm efficiency metrics of dairy cows based on body weight and milk solids yield

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ABSTRACT

Milk solids per kilogram of body weight (BW) is growing in popularity as a measure of dairy cow lactation efficiency. Little is known on the extent of genetic variability that exist in this trait but also the direction and strength of genetic correlations with other performance traits. Such genetic correlations are important to know if producers are to consider actively selecting cows excelling in milk solids per kilogram of BW. The objective of the present study was to use a large data set of commercial Irish dairy cows to quantify the extent of genetic variability in milk solids per kilogram of BW and related traits but also their genetic and phenotypic inter-relationships. Mid-lactation BW and body condition score (BCS), along with 305-d milk solids yield (i.e., fat plus protein yield) were available on 12,413 lactations from 11,062 cows in 85 different commercial dairy herds. (Co)variance components were estimated using repeatability animal linear mixed models. The genetic correlation between milk solids and body weight was only 0.05, which when coupled with the observed large genetic variability in both traits, indicate massive potential to select for both traits in opposite directions. The genetic correlations between both milk solids and BW with BCS; however, need to be considered in any breeding strategy. The genetic standard deviation, heritability, and repeatability of milk solids per kilogram of BW was 0.08, 0.37, and 0.57, respectively. The genetic correlation between milk solids per kilogram of BW with milk solids, BW, and BCS was 0.62, −0.75, and −0.41, respectively. Therefore, based on genetic regression, each increase of 0.10 units in genetic merit for milk solids per kilogram of BW is expected to result in, on average, an increase in 16.1 kg 305-d milk solids yield, a reduction of 25.6 kg of BW and a reduction of 0.05 BCS units (scale of 1–5 where 1 is emaciated). The genetic standard deviation (heritability) for 305-d milk solids yield adjusted phenotypically to a common BW was 27.3 kg (0.22). The genetic correlation between this adjusted milk solids trait with milk solids, BW, and BCS was 0.91, −0.12, and −0.26, respectively. Once also adjusted phenotypically to a common BCS, the genetic standard deviation (heritability) for milk solids adjusted phenotypically to a common BW was 26.8 kg (0.22) where the genetic correlation with milk solids, BW and BCS was 0.91, −0.21, and −0.07, respectively. The genetic standard deviation (heritability) of BW adjusted phenotypically for differences in milk solids was 35.3 kg (0.61), which reduced to 33.2 kg when also phenotypically adjusted for differences in BCS. Results suggest considerable opportunity exists to change milk solids yield independent of BW, and vice versa. The opportunity is reduced slightly once also corrected for differences in BCS. Inter-animal BCS differences should be considered if selection on such metrics is contemplated.

Key words: weight, condition, milk solids, residual solids

INTRODUCTION

Efficiency of production in agriculture, whatever the species, is a topic not only of growing interest in the scientific literature (Veerkamp, 1998; Berry and Crowley, 2013) but also among producers and consumers. A whole plethora of different efficiency measures exist in lactating dairy cows (Vallimont et al., 2011; Pryce et al., 2015; Hurley et al., 2016), each with their own specific advantages and disadvantages. Although the importance of considering some measure of ingested energy (e.g., feed intake, DMI, energy intake) in any efficiency metric is undisputed, the feasibility of collecting vast quantities of such data on individual cows is questionable given the current state of the art. Hence, there is an interest in other more readily accessible measures of efficiency while, at the same time, acknowledging these are not optimal.

One metric sometimes used by producers is the kilogram of lactation yield per kilogram of cow (metabolic)

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BW (Macdonald et al., 2008; Prendiville et al., 2009; Coleman et al., 2010; Lembeye et al., 2016). Lactation yield here could imply total milk yield (e.g., liquid milk market), kilograms of milk solids or fat plus protein yield (e.g., manufacturing milk), or indeed either a reflection of the calorific content of the milk (e.g., net energy of lactation; NRC, 2001) or the economic value of the milk. Little is known of the phenotypic or genetic correlations between milk solids per kilogram of BW and other performance traits, most notably BW, milk solids, and BCS. Using a population of 1,412 Holstein-Friesian dairy cows, Hurley et al. (2016) estimated a phenotypic correlation of 0.73 between net energy of lactation per kilogram of metabolic BW with energy conversion efficiency (i.e., net energy of lactation per unit net energy intake). The corresponding genetic correlation between net energy of lactation per kilogram of metabolic BW across lactation varied from 0.53 to 0.91 (Hurley et al., 2017). This implies that genetic selection for milk solids per kilogram of BW should, on average, improve energy and feed conversion efficiency per lactation through indirect selection.

Although feed conversion efficiency cannot readily be measured in commercial herds, milk solids per kilogram of BW can. The ability to easily calculate milk solids per kilogram of BW per cow is therefore contributing to a narrative that selection on such a metric could lead to improved efficiency. This is despite the inclusion of both milk production and BW in most dairy cow breeding objectives in developed countries (Berry et al., 2007b; Cole and VanRaden, 2018). Nonetheless, there is an interest on generating estimates of genetic merit for milk solids per kilogram of BW as a supplementary measure to ranking on an overall breeding goal. Interbreed differences in milk solids per kilogram of BW have been reported in lactating dairy cows (Prendiville et al., 2009; Lembeye et al., 2016). Whether intra-breed genetic variation in milk solids per kilogram of BW actually exists is still unknown, let alone the effect of such a selection strategy on the selection pressure on other traits.

The objective of the present study was to estimate variance components for milk solids per kilogram of BW but also to explore other metrics using both individual component traits (i.e., BW and milk solids) without necessarily having to resort to a ratio trait such as milk solids per kilogram of BW. Also of interest was the effect of selection on BCS, a trait known to be associated with both BW and milk production in most dairy cow populations (Koenen and Veerkamp, 1998; Berry et al., 2003; Toshniwal et al., 2008) but also a trait well documented to be both phenotypically (Roche et al., 2009) and genetically (Pryce et al., 1998; Berry et al., 2003; Dechow et al., 2004) correlated with dairy cow health and fertility.

MATERIALS AND METHODS

All data were extracted from the Irish Cattle Breeding Federation (http://www.icbf.com) database. A total of 39,610 BW observations recorded on the same day as a BCS assessment were available from 31,069 cows in 163 Irish herds between the years 2018 and 2020, inclusive. All herds considered had to have data from at least 50 cows. Body weight was recorded using a weighing scale, whereas BCS was assessed on a 1 (emaciated) to 5 (obese) scale (Edmonson et al., 1989). Both traits were recorded either by producers themselves or by 2 hired technicians. The data collection procedures and quality control applied are described in detail by Berry and Kelleher (2021). Only data from parities 1 to 15 were retained. Parity number was recoded as 1, 2, 3, 4, and 5+. The only records considered further were from cows that were weighed in the same herd that they last calved in as well as having been in that herd for at least 100 d. A single BW and corresponding BCS record was retained per lactation The BW and corresponding BCS record closest to mid lactation was retained. Based on the frequency distribution of the data, mid lactation in the present study was represented by 14 d each side of 145 DIM. Hence, only BW (and BCS) records in this interval were retained.

Only data from parities with an associated 305-d milk production value were retained. Milk production information included 305-d milk, fat, and protein yield. The sum of fat plus protein yield was calculated and will herein be referred to as milk solids yield (kg). Obvious erroneous data were discarded. Milk solids per kilogram of BW (unitless) was defined as 305-d milk solids yield divided by mid-lactation BW.

Animals were assigned to contemporary groups for use in the subsequent statistical model in an attempt to remove nuisance variability. Contemporary group in the present study was defined as herd-year-season of calving based on the developed algorithm used for most of the national genetic evaluations in Ireland (Berry et al., 2013). Only contemporary groups with at least 10 records were considered further where the difference in calving date between the start and end of the contemporary group was no longer than 30 d. Following all edits, BW, BCS, and milk production data were available from 12,413 lactations from 11,062 cows in 206 contemporary groups from 85 different dairy herds. The mean number of lactation records per herd was 146. The proportion of records per parity was 0.25, 0.21, 0.17, 0.14, and 0.23 for parity 1 through to 5+, respectively.

Of the edited data set, 51% had some recorded Jersey bloodline with the remainder being Holstein-Friesian; the average proportion of Jersey in the cows was 0.17.

Statistical Analyses

Variance components for BW, BCS, milk solids, and milk solids per kilogram of BW were estimated using repeatability animal linear mixed models in ASReml (Gilmour et al., 2009):

$$Y_{ijk} = CG_j + \text{het} + \text{rec} + parity_k + \text{days} + a_i + pe_i + e_{ijk},$$

where Y_{ijk} is the dependent variable of milk solids, BW, BCS, or milk solids per kilogram of BW for animal i; CG_j is the jth contemporary group of herd-year-season of calving; het is the regression coefficient on heterosis (VanRaden and Sanders, 2003); rec is the regression coefficient on recombination loss (VanRaden and Sanders, 2003); $parity_k$ is parity k of the cow, days is the regression coefficient on DIM relative to 145 DIM (not fitted when the dependent variable was milk production); a_i is the random additive genetic effect of animal i, $a \sim N\left(\mathbf{Qg}, \mathbf{A}\sigma_a^2\right)$, where $\mathbf{Q}$ is a matrix relating a to genetic groups, $\mathbf{g}$ is a vector of genetic group means, $\mathbf{A}$ is the numerator relationship matrix, and σ_a^2 is the additive genetic variance; pe_i is the random permanent environmental effect of animal i across lactations $N\left(0, \mathbf{I}\sigma_{pe}^2\right)$, where σ_{pe}^2 is the permanent environmental variance and $\mathbf{I}$ is the identity matrix; and e_{ijk} represents the residual term, where $N\left(0, \mathbf{I}\sigma_e^2\right)$ with σ_e^2 representing the residual variance and $\mathbf{I}$ an identity matrix. The pedigree of all animals was traced back to the founder population who, in turn, were allocated to genetic groups based on breed. The number of animals in the pedigree was 80,761.

In a series of follow-up analyses, 3 different sets of covariates were included in the statistical model for each dependent variable. When the dependent variable was BW, 3 different combinations of milk solids and BCS were included as covariates. When milk solids alone was included as a covariate (along with the aforementioned fixed and random terms described previously) the trait is referred to as $\mathbf{BW_{MS}}$; when BCS alone was included in the model the trait is referred to as $\mathbf{BW_{BCS}}$; when both milk solids and BCS were included in the model the trait is referred to as $\mathbf{BW_{MS,BCS}}$. When the dependent variable was milk solids, 3 different combinations of BW and BCS were included as covariates in the model. When BW alone was included as a covariate (along with the aforementioned fixed and random terms described previously) the trait is referred to as $\mathbf{MS_{BW}}$; when BCS alone was included in the model the trait is referred to as $\mathbf{MS_{BCS}}$; when both BW and BCS were included in the model, the trait is referred to as $\mathbf{MS_{BW,BCS}}$. Genetic, residual, permanent environmental and phenotypic covariances were estimated among all traits using a series of bivariate animal linear mixed models. The variance component estimates using this approach were almost identical to those estimated from a 2-step model that first pre-adjusted the dependent variable for the covariate(s) and then estimated the variance components for the resulting model residuals. The heritability of each trait was defined as the ratio of the genetic variance to the phenotypic variance, whereas the repeatability was the ratio of the sum of the genetic variance and permanent environmental variance relative to the total phenotypic variance.

RESULTS

Summary statistics for the different traits investigated in the present study are in Table 1. Mean (SD) BW of the cows was 526 (72) kg, whereas the mean (SD) BCS was 2.96 (0.27) units. Cows were, on average, 145 d postcalving when weighed. Mean (SD) 305-d milk solids yield was 503 (92) kg and mean (SD) milk solids per kilogram of BW was 0.96 (0.16). All variables were normally distributed. The heterosis coefficient model solutions for BW and BCS was 6.87 (SE = 2.80) kg and 0.05 (SE = 0.01) units, respectively; the recombination loss coefficient estimate for BW was −17.24 (SE = 4.78) with no association detected for BCS. Heterosis estimates for milk solids per kg of BW and $\text{MS}_{\text{BW,BCS}}$ was 0.02 (SE = 0.008) and 26.3 (SE = 3.6) kg, respectively, with no association detected between the heterosis coefficient and $\text{BW}_{\text{MS,BCS}}$. Recombination loss coefficient estimates for milk solids per kilogram of BW and $\text{BW}_{\text{MS,BCS}}$ was 0.04 (SE = 0.014) and −16.92 kg (SE = 4.37), respectively, with no association detected for $\text{MS}_{\text{BW,BCS}}$. Heritability estimates varied from 0.21 (milk solids and MS_{BCS}) to 0.64 (BW_{BCS}). Heritability of the traits related to BW varied from 0.61 to 0.64. Repeatability estimates for the different traits varied from 0.46 ($\text{MS}_{\text{BW,BCS}}$) to 0.86 (BW) with the repeatability of all BW related traits varying from 0.83 to 0.86. The genetic standard deviation for the BW traits varied from 33.2 kg for $\text{BW}_{\text{MS,BCS}}$ to 35.4 kg for BW. This suggests little phenotypic contribution of milk solids or BCS to differences in BW. A similar conclusion was evident for milk solids with the genetic standard deviation of milk solids being 27.0 kg but only reducing to 26.4 kg when phenotypic differences in BCS were accounted for.

Table 1. Phenotypic (σ_p) and genetic (σ_g) standard deviation as well as heritability (h^2) and repeatability (t) estimates (SE in parentheses)

Trait[1]	σ_p	σ_g	h^2	t
BW (kg)	45.4	35.4	0.61 (0.03)	0.86 (0.01)
BW_{MS} (kg)	45.1	35.3	0.61 (0.03)	0.85 (0.01)
$BW_{MS,BCS}$ (kg)	41.5	33.2	0.64 (0.03)	0.83 (0.01)
BW_{BCS} (kg)	42.3	33.6	0.63 (0.03)	0.85 (0.01)
BCS (1–5 scale)	0.23	0.13	0.31 (0.03)	0.54 (0.02)
Milk solids (kg)	58.9	27.0	0.21 (0.02)	0.48 (0.02)
Milk solids per kg of BW	0.13	0.08	0.37 (0.03)	0.57 (0.02)
MS_{BW} (kg)	58.5	27.3	0.22 (0.02)	0.48 (0.02)
$MS_{BW,BCS}$ (kg)	57.4	26.8	0.22 (0.02)	0.46 (0.02)
MS_{BCS} (kg)	58.2	26.4	0.21 (0.02)	0.48 (0.02)

[1] BW_x is residual BW adjusted for milk solids (MS), BCS, or both; MS_x is residual milk solids adjusted for BW, BCS, or both.

Phenotypic and genetic correlations among the traits investigated are in Table 2. Body weight was moderately correlated with BCS both phenotypically (0.37) and genetically (0.33). The phenotypic (0.11) and genetic (0.05) correlations between BW and milk solids were close to zero. The genetic correlation between milk solids per kilogram of BW with both BW (−0.75) and milk solids yield (0.62) were moderate to strong yet in an opposite direction. The genetic correlation between milk solids per kilogram of BW and BCS was −0.41 with a similar phenotypic correlation of −0.35. These genetic and phenotypic correlations therefore suggest that selection alone for improved milk solids per kilogram of BW will, on average, result in poor mid-lactation BCS.

Genetic and phenotypic correlations between BW and the adjusted BW traits (i.e., BW_{MS}, BW_{BCS}, $BW_{MS,BCS}$) of ≥0.988 signify that they were almost identical traits. The existence of near unity correlations was less of a case between milk solids and its adjusted traits (i.e., MS_{BW}, MS_{BCS}, $MS_{BW,BCS}$) where the phenotypic correlations among these traits ranged from 0.93 to 0.97, whereas the range in the corresponding genetic correlations was 0.86 to 0.91.

The standard error of the genetic correlation between MS_{BW} (i.e., milk solids adjusted phenotypically for BW) and BW was more than half the genetic correlation (−0.12), whereas the phenotypic correlation was near zero (0.01) signifying no effect, on average, between selection on MS_{BW} and BW. Incidentally the only way the phenotypic correlation could not be zero is if the genetic covariance was negative and the residual covariance was positive. Although selection for MS_{BW} alone is expected to reduce BCS (genetic correlation of −0.26), selection on $MS_{BW,BCS}$ is expected to have no effect (genetic correlation of −0.06) on BCS although it should still reduce BW (genetic correlation of −0.15). Both MS_{BW} and $MS_{BW,BCS}$, as well as MS_{BCS}, were strongly genetically correlated with milk solids per kilogram of BW (0.65–0.74; Table 2)

DISCUSSION

Volatility in global milk price coupled with greater external pressures on reducing the effect of ruminant production on the environment and available resources (e.g., human edible foodstuffs) has motivated producers to examine, in more detail, the efficiency of production. Although ranking animals on overall lifetime efficiency is the pinnacle, it is currently not feasible for the overwhelming majority of commercial dairy herds. Producers tend to latch onto concepts that are easy to understand and can be readily calculated at both a cow level and herd level, facilitating both benchmarking and target setting. One such trait is milk solids lactation yield per kilogram of average lactation BW. Both milk solids and BW can be readily measured on farm and, all else being equal, increasing the ratio is deemed to be favorable (Macdonald et al., 2008; Prendiville et al., 2009; Lembeye et al., 2016). Nevertheless, single-trait selection is no longer advocated but instead, should be undertaken within the framework of an overall breeding goal. Many breeding goals already include both component traits and, if the weighting on both traits is correct, then optimal gain in overall performance should be achievable through selection on that breeding goal without consideration of any additional trait. This was clearly demonstrated in New Zealand for milk solids per kilogram of BW where simultaneous selection for increased milk solids and lighter cows was pursued within the framework of their national breeding objective (Harris et al., 2007). Although some producers may argue (correctly) that national or breed-specific breeding goals are only optimal for the system representing the assumptions used to derive the weighting factors, customized selection indices offer an opportunity to

Table 2. Genetic (above diagonal; SE in parentheses) and phenotypic (below diagonal) correlations between the different traits investigated

Trait[1]	BW	BW_{MS}	$BW_{MS,BCS}$	BW_{BCS}	BCS	Milk solids	MS_wt	MS_{BW}	$MS_{BW,BCS}$	MS_{BCS}
BW		0.999 (0.0001)	0.998 (0.0002)	0.988 (0.02)	0.33 (0.05)	0.05 (0.06)	−0.75 (0.03)	−0.12 (0.06)	−0.15 (0.06)	0.15 (0.06)
BW_{MS}	0.99		0.97 (0.004)	0.998 (0.0002)	0.35 (0.05)	−0.01 (0.06)	−0.79 (0.02)	−0.18 (0.06)	−0.21 (0.06)	0.07 (0.06)
$BW_{MS,BCS}$	0.99	0.93		0.996 (0.001)	0.10 (0.05)	0.02 (0.06)	−0.75 (0.03)	−0.14 (0.06)	−0.23 (0.06)	0.04 (0.06)
BW_{BCS}	0.99	0.995	0.99		0.15 (0.05)	0.11 (0.06)	−0.72 (0.03)	−0.06 (0.06)	−0.14 (0.06)	0.13 (0.06)
BCS	0.37	0.39	0.03	0.10		−0.20 (0.07)	−0.41 (0.05)	−0.26 (0.07)	−0.06 (0.07)	−0.03 (0.08)
Milk solids	0.11	0.01	0.01	0.17	−0.14		0.62 (0.04)	0.91 (0.02)	0.91 (0.02)	0.86 (0.03)
MS_wt	−0.52	−0.60	−0.56	−0.48	−0.35	0.77		0.74 (0.03)	0.75 (0.03)	0.65 (0.04)
MS_{BW}	0.01	−0.09	−0.08	0.08	−0.18	0.97	0.83		0.96 (0.01)	0.85 (0.06)
$MS_{BW,BCS}$	0.02	−0.08	−0.14	0.02	−0.01	0.96	0.81	0.97		0.86 (0.02)
MS_{BCS}	0.19	0.07	0.02	0.18	0.00	0.93	0.80	0.99	0.93	

[1] BW_x is residual BW adjusted for milk solids, BCS, or both; MS_wt is milk solids per kilogram of BW; MS_x is residual milk solids adjusted for BW, BCS, or both.

modify the breeding goals to suit each farm. The decomposition of overall breeding goals into subindices (Berry et al., 2007b; Cole and VanRaden, 2018) also facilitates the adjustment of relative weights on different suites of traits. Irrespective, demand still exists for genetic evaluations of additional traits such as milk solids per kilogram of BW. A precedence already exists for such a demand in dairy cattle with linear type traits not explicitly included in several dairy cow breeding goals (Cole and VanRaden, 2018), yet standalone measures of genetic merit for these traits are published alongside the breeding goal values of animals.

Milk solids per kilogram of BW is proposed as a measure of gross feed efficiency. Milk solids per kilogram of BW is designed to reflect animals that are expected to partition more energy to milk solids output as opposed to cow maintenance assuming no difference in feed intake. Although differences in net efficiency among dairy cows do exist (Fischer et al., 2018), multiple regression statistical models developed in lactating dairy cows that include the independent variables of BW (change) and milk production variables tend to explain a large proportion of the variability in feed intake (Coleman et al., 2010; Fischer et al., 2018). The relevance of milk solids per kilogram of BW is particularly true in grazing production system where the feed available is fixed and thus, there is a desire that a greater proportion is used for milk production as opposed to cow maintenance. Results from the present study clearly points to the existence of considerable exploitable genetic variability in milk solids per kilogram of BW. The observed genetic standard deviation for $MS_{BW,BCS}$ suggests that the mean difference in milk solids between the top and bottom 20% of animals genetically, while holding BW and BCS constant, is 75 kg representing 15% of the phenotypic mean for milk solids. The high heritability (0.37) and repeatability (0.57) of milk solids per kilogram of BW implies that accurate EBV are possible, even for ungenotyped cows. Ignoring genomic and parental information, one lactation record would achieve a reliability of 0.37, whereas 2 and 5 lactations would equal a reliability of 0.47 and 0.56, respectively. Nevertheless, the presented correlations with BCS imply that any single-trait selection should be undertaken with caution.

Of note is the difference in energetic cost of producing a kilogram of fat versus protein (O'Mara, 1996), but more importantly the difference in economic value of a kilogram of fat versus protein implies that alternative strategies to simply summing fat and protein yield to generate the milk solids variable could be considered. The actual relative weight on the 2 milk components is dependent on the jurisdiction and the market destination (e.g., liquid, cheese) of the milk produced.

Study Motivation

One of the motivations for the present study was to first quantify the extent of genetic variability in milk solids per kilogram of BW, but importantly, because higher genetic merit for milk (solids) yield is generally accompanied by poorer BCS (Berry et al., 2003; Toshniwal et al., 2008; Bilal et al., 2016), as well as lighter animals (Berry et al., 2003; Pryce and Harris, 2006; Toshniwal et al., 2008), one hypothesis was that selection for improved milk solids per kilogram of BW ratio may have repercussions for BCS. Thus, although selection for improved milk solids/energy per kilogram of BW may relate to improved efficiency on a per lactation basis (Prendiville et al., 2009; Hurley et al., 2016), the known genetic (Pryce et al., 1998; Berry et al., 2003; Dechow et al., 2004) and phenotypic (Berry et al., 2007a; Roche et al., 2007) association between BCS and fertility, health, and survival may lead to an unfavorable association between milk solids per kilogram of BW and lifetime efficiency. In fact, results from the present study indeed reveal that selection alone for greater milk solids per kilogram of BW will, on average, reduce BCS (genetic correlation of −0.41 between milk solids per kilogram of BW and BCS; Table 2) manifesting itself via a negative genetic correlation of −0.20 between milk solids and BCS and a positive genetic correlation of 0.33 between BW and BCS. Negative genetic correlations between milk (solids) yield and BCS have been reported in most other dairy cow populations (Veerkamp et al., 2001; Berry et al., 2003; Toshniwal et al., 2008), with some exceptions (Pryce and Harris 2006). Similarly, moderate positive genetic correlations between BW and BCS have been reported in dairy cows (Veerkamp and Brotherstone, 1997; Berry et al., 2002; Toshniwal et al., 2008), prompting Veerkamp (1998) to caution against selection blindly for lighter cows. Based on the variance components estimated in the present study, each 50-kg increase in genetic merit for milk solids (through single-trait selection) is expected to reduce genetic merit for BCS of 0.05 units (1–5 scale). Each 50 kg lighter genetic merit for mid-lactation BW (through single-trait selection) is expected to reduce genetic merit for BCS by 0.06 units (1–5 scale). Again, using the population parameters estimated in the present study, each genetic standard deviation improvement in milk solids per kilogram of BW (from single-trait selection) should equate to a genetically 26.5 kg lighter cow producing 16.7 kg more milk solids but of 0.05 BCS units less. These estimates from the present study are, however, all within breed and differences may exist if the pursuit of improving milk solids per kilogram of BW was achieved through breed substitution or crossbreeding, such as with breeds such as the Jersey (Prendiville et al., 2009; Lembeye et al., 2016). From a controlled Irish study of 110 Holstein-Friesian, Jersey, and Holstein-Friesian × Jersey crossbreds, Prendiville et al. (2009) reported greater BCS in Jersey cows despite being 129 kg lighter. The Jersey purebreds also had the highest milk solids per kilogram of BW. From a controlled study of once-a-day milking in New Zealand, Lembeye et al. (2016) reported superior milk solids per kilogram of BW in purebred Jersey cows relative to Holstein-Friesians or their crosses (Jersey was 83 kg lighter than the Holstein-Friesian but produced 25.6 kg less milk solids), but the Jersey cows were of lower BCS than the crossbreds but the same as the Holstein-Friesians.

Producers generally select from candidate sires ranking relatively high on the overall breeding goal. Ancillary information such as suitability for the particular production system, suitability for heifers, breed, conformation, and semen price are then used in narrowing the eventual selection; it is here where traits such as milk solids per kilogram of BW would also be used. The effect of truncation selection on genetic gain using this approach is likely to be relatively small because the candidate sires already rank highly on the breeding goal. This effect would especially be true for milk solids per kilogram of BW given that breeding objectives target greater milk production with many also having a negative weight on cow size (Berry et al., 2007b; Cole and VanRaden, 2018). Nonetheless, the potential small effect of truncation selection in this strategy is conditional on the breeding objective including most traits of economic importance, which is not particularly true for many health and resilience traits, which are known to be correlated with BCS (Pryce et al., 1998; Dechow et al., 2004). Nevertheless, a more pressing issue could exist in the selection of dams-to-dams pathway. Many farmers now weigh their cows in mid lactation and, based on the recorded BW coupled with the milk solids output, the cows are ranked on milk solids per kilogram of BW. Aggressive selection can then be imposed on this metric and although genetic gain in the cow population follows that of the other selection pathways (with some lag), this strategy can be important to the extent of that lag (Dechow and Rogers, 2018). Given the heritability and repeatability of 0.37 and 0.57, respectively for milk solids per kilogram of BW in the present study (Table 1), mass selection can be quite effective thus potentially having an unfavorable effect on BCS. Both BCS and BW in dairy cows reach nadir in mid lactation (Berry et al., 2006b) and, based on an analysis of 7,391 multiparous Irish dairy cows, Berry et al. (2011) documented how each BCS unit (also assessed on a 1–5 scale) equated to, on average, 39 kg of BW; a similar exercise has been undertaken for BCS on a 1 to 10 scale (Berry et al., 2006a). Hence, consideration does need to be made of the BCS of the cow when weighing. Nonetheless, pre-adjusting the BW data for differences in BCS through the addition or subtraction of 39 kg/unit deviation in BCS from the population mean only weakened the genetic correlation between milk solids per kilogram of BW and BCS from −0.41 to −0.31. The associated phenotypic correlation between milk solids per kilogram of BW and BCS weakened from −0.35 to −0.23 following adjustment for a set BW value of 39 kg/unit of BCS. This unfavorable phenotypic and genetic relationship between milk solids per kilogram of BW with BCS was one motivation for the evaluation of other similar traits in the present study, but that also considered the BCS of the cow when weighed.

Alternative Concepts Still Based on Milk Solids and BW

Several disadvantages exist for the milk solids per kilogram of BW trait despite it being normally distributed: (1) it is a ratio trait thus suffering from the associated statistical properties of ratio traits (Sutherland, 1965; Gunsett, 1984), (2) because it is a ratio trait with the same units of measure in the numerator and denominator, it is unitless, (3) such a ratio trait does not accommodate the use of different economic weights on each of the component traits (i.e., the ratio of the economic weights on both traits is constant per animal), and (4) it is unfavorably associated with BCS, with likely repercussions for animal health, fertility, and longevity (Pryce et al., 1998; Dechow et al., 2004).

The main statistical disadvantages of a ratio trait such as milk solids per kilogram of BW as part of a breeding program owes itself to the moderate to strong correlations between the ratio trait and its component traits (genetic correlations of 0.62 and −0.75 with milk solids yield and BW in the present study) due to the part-whole relationship that exists. Because of this, the expected response to selection on ratio traits is difficult to predict (Gunsett, 1984) because desirable responses can occur in either the numerator or the denominator and their relative selection pressures are unknown. Sutherland (1965) demonstrated that a disproportionate selection pressure will be exerted on the trait in the ratio with the greater genetic variance. In the present study, the coefficient of genetic variation for milk solids yield and BW was 5.3 and 6.7%, respectively. These coefficient of variation estimates are relatively consistent with estimates in other dairy cow populations for BW and milk (solids) yield (Veerkamp and Brotherstone, 1997; Berry et al., 2002; Toshniwal et al., 2008). Nonetheless, selection for greater milk solids yield will improve milk solids per kilogram of BW because of the genetic correlation of 0.62 that exists between both traits with the same being true of BW. In fact, using the equation described by Sutherland (1965) on estimating the genetic correlation between a ratio trait and the denominator given the population parameters, the expected genetic correlation between milk solids per kilogram of BW with BW was −0.77, which is almost identical to the −0.75 estimated directly from the data in the present study. When the genetic variation in BW is greater than that of milk solids, then the genetic correlation between BW and milk solids per kilogram of BW will always be strong. Nonetheless, the coefficient of genetic variation for BW is not necessarily always greater than that for milk yield (Veerkamp and Brotherstone, 1997; Toshniwal et al., 2008).

The unit of measure of milk solids and BW is both kg. Hence, the ratio of milk solids and BW is unitless, which can make it somewhat difficult to interpret biologically. For example, the ratio of a 450-kg cow yielding 450 kg of milk solids is the same as that of a 500-kg cow yielding 500 kg of milk solids. This is why having access to the individual EBV can be more beneficial, as is the case when included in the overall breeding objective. Nonetheless, although one of the objectives of the adjusted BW (i.e., BW_{MS}, BW_{BCS}, $BW_{MS,BCS}$) and milk solids (i.e., MS_{BW}, MS_{BCS}, $MS_{BW,BCS}$) traits was to circumvent the unfavorable statistical properties of a ratio trait, it was also to generate a value in either kilograms of milk solids or kilograms of BW relative to the expected value given the sample population and simultaneously accounting for the other contributing effects such as parity. For example, an EBV for adjusted milk solids of +30 kg implies that, after adjusting for nuisance factors, the cow is expected to yield 30 kg more milk solids than expected given her BW. How this was actually achieved is not clear, especially as no feed intake data were used in the calculation because it is not routinely available. Nonetheless, the correlation between BW and intake in dairy cows is 0.28 to 0.53 (Toshniwal et al., 2008; Hurley et al., 2016). An additional advantage of the adjusted BW and traits is that they can also be simultaneously adjusted for BCS, thus reducing the potential indirect effect on BCS from selection for lighter cows as evidenced by the lack of a genetic correlation between either $BW_{MS,BCS}$ or $MS_{BW,BCS}$ with BCS. The approach of deriving $BW_{MS(BCS)}$ and $MS_{BW(BCS)}$ in the present study is analogous to the commonly cited residual feed intake in cattle (Byerly, 1941). Coleman et al. (2010) also defined residual feed intake in lactating dairy cows but also defined a trait they called residual solids production which is similar in technique to $MS_{BW(BCS)}$ in the present study except that feed intake was also included as an independent variable in the definition by Coleman et al., (2010). Although most studies traditionally first estimate these residual traits (as the residual from the fitted model) and then undertake a genetic analysis, the present study did this in one step which is now more the norm (Savietto et al., 2014). The resulting parameter estimates were almost identical to if undertaken using the traditional 2-step approach (results not shown). Furthermore, phenotypic regression was used in the present study to adjust BW for differences in milk solids (and BCS), and vice versa. Adjustment could equally be undertaken using genetic regression and (within breed) genetic independence between the residuals and independent variables could then be guaranteed. It should also be noted that although independence exists between the residuals from a model and the independent variables within the entire population, this may not necessarily hold true for subpopulations (e.g., selected animals).

Berry and Crowley (2012) proposed the amalgamation of 2 efficiency measures and, in doing so, reaped the benefits of each of the individual measure. In the present study, selection for reduced $BW_{MS,BCS}$ is expected to reduce BW with no effect on either BCS or milk solids. Selection for greater $MS_{BW,BCS}$, on the other hand, is expected to increase milk solids with no effect on BCS and only a small effect on reducing BW. Analogous to the definition of residual intake and gain (combination of residual feed intake and residual gain in growing animals; Berry and Crowley, 2012), combining $BW_{MS,BCS}$ and $MS_{BW,BCS}$ could achieve a dual objective of increasing milk solids and reducing BW without any effect on BCS or without having to resort to a ratio trait such as milk solids per kilogram of BW. The genetic correlation between $BW_{MS,BCS}$ and $MS_{BW,BCS}$ is only −0.23 indicating that they are distinctly different measures.

Although the objective of the present study was to quantify the feasibility and likely gains of genetic selection for some combination of milk solids, BW (and BCS), the contemporary group effect solutions from the genetic evaluation model (best linear unbiased estimates; **BLUE**) are also growing in popularity as a herd management tool (Dunne et al., 2019). Herd-level BLUE are measures independent of genetic merit of the herd, and thus herds with inferior BLUE for efficiency metrics can be alerted of such and, if appropriate, remedial measures put in place.

In conclusion, considerable (genetic) variability exists in milk solids output relative to BW; alternative strategies exist to define such a metric and these metrics could be modified further to reflect the different energetic cost or economic value of the respective component traits. Consideration should, however, be taken of differences in BCS differences among cows so as to try and minimize or alleviate the effect of selection on such traits on the mean BCS of the population; this is important as (1) not all traits (e.g., health) associated with BCS are generally included in total merit indexes, (2) the energetic release from the catabolism of BCS is less than the energetic cost of regaining that lost BCS (O'Mara, 1996), and (3) in some production systems (e.g, New Zealand; Byrne et al., 2013), there is an explicit economic value on BCS because of its influence on the decision to dry off cows. Nonetheless, the evidence is overwhelming that selection on a linear combination of the traits that make up a ratio is more efficient than selection on the ratio itself (Gunsett, 1984; Zetouni et al., 2017).

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REFERENCES

Berry, D. P., F. Buckley, and P. Dillon. 2011. Relationship between live weight and body condition score in Irish Holstein-Friesian dairy cows. Ir. J. Agric. Food Res. 50:141–147.

Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2002. Genetic parameters for level and change of body condition score and body weight in dairy cows. J. Dairy Sci. 85:2030–2039. https://doi.org/10.3168/jds.S0022-0302(02)74280-X.

Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2003. Genetic parameters for body condition score, body weight, milk yield, and fertility estimated using random regression models. J. Dairy Sci. 86:3704–3717. https://doi.org/10.3168/jds.S0022-0302(03)73976-9.

Berry, D. P., and J. J. Crowley. 2012. Residual intake and body weight gain: A new measure of efficiency in growing cattle. J. Anim. Sci. 90:109–115. https://doi.org/10.2527/jas.2011-4245.

Berry, D. P., and J. J. Crowley. 2013. Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. J. Anim. Sci. 91:1594–1613. https://doi.org/10.2527/jas.2012-5862.

Berry, D. P., J. F. Kearney, K. Twomey, and R. D. Evans. 2013. Genetics of reproductive performance in seasonal calving dairy cattle production systems. Ir. J. Agric. Food Res. 52:1–16.

Berry, D. P., and M. M. Kelleher. 2021. Differences in genetic merit for visually-assessed body condition score materialises as phenotypic differences in tactile-based body condition score in commercial dairy cows. Animal 15:100181. https://doi.org/10.1016/j.animal.2021.100181.

Berry, D. P., J. M. Lee, K. A. Macdonald, K. Stafford, L. Matthews, and J. R. Roche. 2007a. Associations among body condition score, body weight, somatic cell count, and clinical mastitis in seasonally calving dairy cattle. J. Dairy Sci. 90:637–648. https://doi.org/10.3168/jds.S0022-0302(07)71546-1.

Berry, D. P., K. A. Macdonald, J. W. Penno, and J. R. Roche. 2006a. Association between body condition score and liveweight in pasture-based Holstein-Friesian dairy cows. J. Dairy Res. 73:487–491. https://doi.org/10.1017/S0022029906002020.

Berry, D. P., L. Shalloo, A. R. Cromie, R. F. Veerkamp, P. Dillon, P. R. Amer, J. F. Kearney, R. D. Evans, and B. Wickham. 2007b. The economic breeding index: A generation on. Technical report to the Irish Cattle Breeding Federation, pp. 1–50. Accessed Jan. 15, 2021. https://www.icbf.com/wp-content/uploads/2013/06/economic_breeding_index.pdf.

Berry, D. P., R. F. Veerkamp, and P. Dillon. 2006b. Phenotypic profiles for body weight, body condition score, energy intake, and energy balance across different parities and concentrate feeding levels. Livest. Sci. 104:1–12. https://doi.org/10.1016/j.livsci.2006.02.012.

Bilal, G., R. I. Cue, and J. F. Hayes. 2016. Genetic and phenotypic associations of type traits and body condition score with dry matter intake, milk yield, and number of breedings in first lactation Canadian Holstein cows. Can. J. Anim. Sci. 96:434–447. https://doi.org/10.1139/cjas-2015-0127.

Byerly, T. C. 1941. Feed and Other Costs of Producing Market Eggs (Bulletin A). University of Maryland, Agricultural Experiment Station.

Byrne, T. J., B. Santos, P. R. Amer, and J. R. Bryant. 2013. The economic value of body condition score in New Zealand seasonal dairying systems. Pages 479–482 in Proc. Assoc. Adv. Anim. Breed Gen., Napier, New Zealand.

Cole, J. B., and P. M. VanRaden. 2018. Possibilities in an age of genomics: The future of selection indices. J. Dairy Sci. 101:3686–3701. https://doi.org/10.3168/jds.2017-13335.

Coleman, J., D. P. Berry, K. M. Pierce, A. Brennan, and B. Horan. 2010. Dry matter intake and feed efficiency profiles of 3 genotypes of Holstein-Friesian within pasture-based systems of milk production. J. Dairy Sci. 93:4318–4331. https://doi.org/10.3168/jds.2009-2686.

Dechow, C. D., and G. W. Rogers. 2018. Genetic lag represents commercial herd genetic merit more accurately than the 4-path selection model. J. Dairy Sci. 101:4312–4316. https://doi.org/10.3168/jds.2017-13571.

Dechow, C. D., G. W. Rogers, U. Sander-Nielsen, L. Klei, T. J. Lawlor, J. S. Clay, A. E. Freeman, G. Abdel-Azim, A. Kuck, and S. Schnell. 2004. Correlations among body condition scores from various sources, dairy form, and cow health from the United States and Denmark. J. Dairy Sci. 87:3526–3533. https://doi.org/10.3168/jds.S0022-0302(04)73489-X.

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. J. Dairy Sci. 102:5295–5304. https://doi.org/10.3168/jds.2018-16119.

Edmonson, A. J., I. J. Lean, L. D. Weaver, T. Farver, and G. Webster. 1989. A body condition scoring chart for Holstein dairy cows. J. Dairy Sci. 72:68–78. https://doi.org/10.3168/jds.S0022-0302(89)79081-0.

Fischer, A., N. C. Friggens, D. P. Berry, and P. Faverdin. 2018. Isolating the cow-specific part of residual energy intake in lactating dairy cows using random regressions. Animal 12:1396–1404.

Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2009. ASREML Reference Manual. New South Wales Agriculture, Orange Agricultural Institute.

Gunsett, F. C. 1984. Linear index selection to improve traits defined as ratios. J. Anim. Sci. 59:1185–1193. https://doi.org/10.2527/jas1984.5951185x.

Harris, B., J. E. Pryce, and W. A. Montgomerie. 2007. Experiences from breeding for economic efficiency in dairy cattle in New Zealand. Proc. Adv. Anim. Breed.Gen. 17:434–444.

Hurley, A. M., N. López-Villalobos, S. McParland, E. Kennedy, E. Lewis, M. O'Donovan, J. L. Burke, and D. P. Berry. 2016. Interrelationships among alternative definitions of feed efficiency in grazing lactating dairy cows. J. Dairy Sci. 99:468–479. https://doi.org/10.3168/jds.2015-9928.

Hurley, A. M., N. López-Villalobos, S. McParland, E. Lewis, E. Kennedy, M. O'Donovan, J. L. Burke, and D. P. Berry. 2017. Genetics of alternative definitions of feed efficiency in grazing lactating dairy cows. J. Dairy Sci. 100:5501–5514. https://doi.org/10.3168/jds.2016-12314.

Koenen, E. P. C., and R. F. Veerkamp. 1998. Genetic covariance functions for live weight, condition score, and dry-matter intake measured at different lactation stages of Holstein Friesian heifers. Livest. Prod. Sci. 57:67–77. https://doi.org/10.1016/S0301-6226(98)00159-6.

Lembeye, F., N. López-Villalobos, J. L. Burke, S. R. Davis, J. Richardson, N. W. Sneddon, and D. J. Donaghy. 2016. Comparative performance in Holstein-Friesian, Jerey and crossbred cows milk once daily under a pasture-based system in New Zealand. N. Z. J. Agric. Res. 59:351–362. https://doi.org/10.1080/00288233.2016.1207669.

Macdonald, K. A., G. A. Verkerk, B. S. Thorrold, J. E. Pryce, J. W. Penno, L. R. McNaughton, L. J. Burton, J. A. S. Lancaster, J. H. Williamson, and C. W. Holmes. 2008. A comparison of three strains of Holstein-Friesian grazed on pasture and managed under different feed allowances. J. Dairy Sci. 91:1693–1707. https://doi.org/10.3168/jds.2007-0441.

NRC. 2001. Energy. Pages 13–27 in Nutrient Requirements of Dairy Cattle. 7th rev. ed. Natl. Acad. Sci.

O'Mara, F. 1996. A net energy system for cattle and sheep. PhD Diss. Department of Animal Science and Production, University College Dublin, Ireland.

Prendiville, R., K. M. Pierce, and F. Buckley. 2009. An evaluation of production efficiencies among lactating Holstein-Friesian, Jersey, and Jersey × Holstein-Friesian cows at pasture. J. Dairy Sci. 92:6176–6185. https://doi.org/10.3168/jds.2009-2292.

Pryce, J. E., R. J. Esslemont, R. Thompson, R. F. Veerkamp, M. A. Kossaibati, and G. Simm. 1998. Estimation of genetic parameters using health, fertility and production data from a management recording system for dairy cattle. Anim. Sci. 66:577–584. https://doi.org/10.1017/S1357729800009152.

Pryce, J. E., O. Gonzalez-Recio, G. Nieuwhof, W. J. Wales, M. P. Coffey, B. J. Hayes, and M. E. Goddard. 2015. Definition and implementation of a breeding value for feed efficiency in dairy cows. J. Dairy Sci. 98:7340–7350. https://doi.org/10.3168/jds.2015-9621.

Pryce, J. E., and B. L. Harris. 2006. Genetics of body condition score in New Zealand dairy cows. J. Dairy Sci. 89:4424–4432. https://doi.org/10.3168/jds.S0022-0302(06)72490-0.

Roche, J. R., N. C. Friggens, J. K. Kay, M. W. Fisher, K. J. Stafford, and D. P. Berry. 2009. Body condition score and its association with dairy cow productivity, health and welfare. J. Dairy Sci. 92:5769–5801. https://doi.org/10.3168/jds.2009-2431.

Roche, J. R., K. A. MacDonald, C. R. Burke, J. M. Lee, and D. P. Berry. 2007. Associations among body condition score, body weight and reproductive performance in seasonal-calving dairy cattle. J. Dairy Sci. 90:376–391. https://doi.org/10.3168/jds.S0022-0302(07)72639-5.

Savietto, D., D. P. Berry, and N. C. Friggens. 2014. Towards an improved estimation of the biological components of residual feed intake in growing cattle. J. Anim. Sci. 92:467–476. https://doi.org/10.2527/jas.2013-6894.

Sutherland, T. M. 1965. The correlation between feed efficiency and rate of gain, a ratio and its denominator. Biometrics 21:739–749. https://doi.org/10.2307/2528555.

Toshniwal, J. K., C. D. Dechow, B. G. Cassell, J. A. D. R. N. Appuhamy, and G. A. Varga. 2008. Heritability of electronically recorded daily body weight and correlations with yield, dry matter intake, and body condition score. J. Dairy Sci. 91:3201–3210. https://doi.org/10.3168/jds.2007-0627.

Vallimont, J. E., C. D. Dechow, J. M. Daubert, M. W. Dekleva, J. W. Blum, C. M. Barlieb, W. Liu, G. A. Varga, A. J. Heinrichs, and C. R. Baumrucker. 2011. Heritability of gross feed efficiency and associations with yield, intake, residual intake, body weight, and body condition score in 11 commercial Pennsylvania tie stalls. J. Dairy Sci. 94:2108–2113. https://doi.org/10.3168/jds.2010-3888.

VanRaden, P. M., and A. M. Sanders. 2003. Economic merit of crossbred and purebred US dairy cattle. J. Dairy Sci. 86:1036–1044. https://doi.org/10.3168/jds.S0022-0302(03)73687-X.

Veerkamp, R. F. 1998. Selection for economic efficiency of dairy cattle using information on live weight and feed intake: A review. J. Dairy Sci. 81:1109–1119. https://doi.org/10.3168/jds.S0022-0302(98)75673-5.

Veerkamp, R. F., and S. Brotherstone. 1997. Genetic correlations between linear type traits, food intake, live weight and condition score in Holstein Friesian dairy cattle. Anim. Sci. 64:385–392. https://doi.org/10.1017/S1357729800015976.

Veerkamp, R. F., E. P. Koenen, and G. De Jong. 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. J. Dairy Sci. 84:2327–2335. https://doi.org/10.3168/jds.S0022-0302(01)74681-4.

Zetouni, L., M. Henryon, M. Kargo, and J. Lassen. 2017. Direct multi-trait selection realizes the highest genetic response for ratio traits. J. Anim. Sci. 95:1921–1925. https://doi.org/10.2527/jas2016.1324.

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