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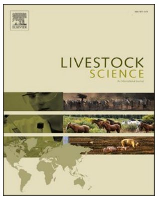

Analysis of milk solids production and mid-lactation bodyweight to evaluate cow production efficiency on commercial dairy farms

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HIGHLIGHTS

- Considerable variation exists between animals within herds and between commercial dairy herds in terms of production efficiency.
- High genetic potential Jersey × Holstein-Friesian crossbred cows showed a greater production efficiency.
- Greater efficiency was characterized by a significant increase in milk solids production and a lower mid-lactation bodyweight.
- Weighing cows routinely will help identify the most efficient dairy cows to breed from to increase the selection intensity on farm.

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ABSTRACT

The efficient production of milk is an important determinant of both, farm productivity and the environmental impact of intensive dairy systems. The objective of the present study was to use a large dataset of commercial dairy cows to determine the relationship among animal breed, Irish total merit index (Economic Breeding Index; **EBI**), parity, and production efficiency parameters, which included milk solids (**MS**) production per kg of mid-lactation bodyweight (**MSperBW**) and the estimated net energy requirement per kg of MS produced (**ENperMS**). Data from 80 different spring-calving commercial dairy herds located in southern Ireland comprising 20,051 cows across 34,002 lactations from Holstein-Friesian (**HF**) and Jersey × Holstein-Friesian crossbred (**JFX**) cows were accessible for the study across 4 years. The data available included individual cow EBI, 305-day MS production, which is kg fat yield plus kg protein yield, calving and dry-off dates, and a mid-lactation bodyweight (**BW**) at 143 ± 26 days in milk. To evaluate the productive efficiency in this study, firstly, individual cow MSperBW was calculated by dividing 305-day MS production by mid-lactation BW, with higher values being desirable (Prendiville et al., 2009; O'Sullivan et al., 2019a). Secondly, ENperMS was established by dividing the total net energy requirement (in Unité Fourragère Lait; **UFL**) for an animal for maintenance (from BW), milk production, and growth (for animals up to lactation 3) by the 305-day MS production (INRA, 2010; Faverdin et al., 2011), where lower values indicate increased efficiency due to lower energy requirement per unit output. Statistical analyses were undertaken using mixed models. Overall, average MSperBW was 0.94 ±0.16 kg MS/ kg BW with large variation between animals within herds (0.42 to 1.47 kg MS/ kg BW) and between herds (0.73 to 1.14 kg MS/ kg BW). Similarly, ENperMS on farm averaged 9.8 total UFL/ kg MS ranging from 9.0 to 10.9 total UFL/ kg MS between farms. The MSperBW was significantly greater for JFX (1.01 kg MS/ kg BW) compared to HF animals (0.92 kg MS/ kg BW), resulting in a reduction in total energy requirements per kg of MS produced (ENperMS) (9.5 vs. 9.8 total UFL/ kg MS for JFX and HF, respectively). Animals with increased MSperBW produced 140 kg/cow more MS per 305-day lactation and were 58 kg lighter than lower MSperBW contemporaries. These results corroborate the benefits of both, selection on EBI and crossbreeding to increase aforementioned production efficiency parameters within intensive grazing systems. The results also provide a further compelling basis for dairy farmers to routinely weigh and milk record their herds to identify more efficient animals on which to increase animal performance and profitability in future generations.

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1. Introduction

The design of a grass-based model within global dairy production systems is indeed peculiar due to its high dependence on natural forces (such as climate) for the production of perishable feed, and grazing animals for the autonomous management of feed quality and utilization (Delaby and Horan, 2017). It is widely acknowledged that the overall integrity of this model of milk production is based on high productivity grassland management in combination with genetically elite animal genotypes capable of compact seasonal calving while efficiently converting grazed grass to milk fat and protein (milk solids; **MS**) (O'Sullivan et al., 2019ba; Delaby et al., 2020). Within such systems, opportunities to increase animal feed efficiency are limited and the amount of milk produced from a given amount of feed is a key measure of both the efficiency and environmental impact of the system (Grainger and Beauchemin, 2011). Increasing pasture allowance to support higher levels of intake and animal performance is inefficient, resulting in higher levels of pasture refusals, reduced pasture utilization and subsequent feed quality (Pérez-Prieto and Delagarde, 2013; Delaby and Horan, 2017), and reduced feed efficiency (Fischer et al., 2020).

Thus, pasture-based industries have commonly developed multi-factor, profit-focused breeding indices with added relative emphasis on such traits as animal fertility, management, maintenance, health, lameness, and longevity to enhance animal performance at grazing (Berry, 2018; Cole and VanRaden, 2018). Such programs have supported substantial improvements in pasture system efficiency and performance, and the dilution of animal maintenance requirements (Roche et al., 2018; Cole and VanRaden, 2018). Indeed, Cole and VanRaden (2018) have recently concluded that the inclusion of estimates of feed efficiency in selection indices worldwide has accelerated the rate of improvement in animal performance. In Ireland, the Economic Breeding Index (**EBI**) was officially launched in 2001 to the Irish dairy industry by the Irish Cattle Breeding Federation (McParland et al., 2008). Although a maintenance sub-index (**Maint SI**) was added in 2010 placing a negative emphasis on bodyweight (**BW**) to reflect the additional costs associated with the maintenance of higher BW animals, the overall contribution of Maint SI is balanced by a beef sub-index (**Beef SI**) to reflect the additional value of larger beef carcasses derived from dairy herds (Berry, 2018).

While a considerable amount of research has been conducted on feed efficiency in growing animals (Archer et al., 1997; Kearney et al., 2004; Wang et al., 2006), there is still a dearth of research for lactating cows within grazing systems (Berry and Crowley, 2013). In addition, the lack of routine cost-effective access to large quantities of feed intake information on individual animals within commercial dairy herds has hindered the further development of robust feed efficiency measures both in terms of pasture-based animal breeding programs and on farm selection intensity. Some studies (Coleman et al., 2010; Berry and Crowley, 2013) have previously focused on and reported significant genetic and phenotypic variation in feed efficiency within pasture-based systems in Ireland. Results from controlled evaluations show a strong relationship (0.7) between efficiency parameters that (1) include dry matter intake (**DMI**) data for calculating the MS production per unit intake (kg MS/ kg DMI); and (2) use the animal's BW to account for cost of maintenance in calculating the MS production per kg BW (kg MS/ kg BW) (Prendiville et al., 2009; O'Sullivan et al., 2019a). But also measures for cow efficiency based on the energy intake derived from individual animal intake data based on the net energy system according to Faverdin et al. (2011) have been evaluated (Coffey et al., 2017; O'Sullivan et al., 2019a). Alternatively, and in virtue of the difficulty of obtaining feed intake data, the use of moderately to highly correlated indicator traits (i.e., MS yield and BW) has been suggested (Köck et al., 2018).

Although a recent study comparing high and average EBI Holstein-Friesian (**HF**), observed similar MS production per unit intake, they found that selection on EBI was contributing to improve the MS production per kg BW (hereafter referred to as **MSperBW**; O'Sullivan et al., 2019a). Similarly, Prendiville et al. (2009) and Coffey et al. (2017) concluded a superior MSperBW for Jersey × Holstein-Friesian crossbred animals (**JFX**) compared to HF. Currently, the average Irish dairy cow has a mature average BW of 650 kg (ICBF, 2019) while the variability in production efficiency due to limitations on the availability of detailed animal intake data on commercial dairy farms has not previously been quantified.

On that basis, the objective of this experiment was to evaluate the relationship among animal genetic merit, parity, breed, and cost-effective production efficiency measures within commercial pasture-based dairy farms in Ireland.

2. Materials and methods

2.1. Data selection

Data from 80 spring-calving commercial dairy herds located in southern Ireland were available from the Irish Cattle Breeding Federation database (http://www.icbf.com) for the years 2016 to 2019 inclusive. These herds were chosen as they had participated in whole herd milk recording and BW measurements during the time period. All of the herds comprised Holstein-Friesian and 64 out of the 80 herds had some Jersey × Holstein-Friesian crossbred dairy cattle as well as other dairy breeds. Therefore, two genetic groups were formed: HF and JFX. For HF, a minimum of 75% of the breed proportion was Holstein-Friesian. On average, the HF cows were 92.5% Holstein-Friesian and < 7% Jersey or other breeds. To define the JFX breed, cows had to have a minimum of 25% of the breed proportion as Jersey. On average, the JFX comprised of 45% Jersey, 50% Holstein and 5% other genetics. The number of cows, number of cow-lactations and average parity of animals available for the study after edits for each breed is presented in Table 1.

The data available included 305-day milk production lactation performance as defined by Olori and Galesloot (1999) [*i.e.*: milk yield (kg), fat yield (kg) and protein yield (kg)], calving date, dry-off date, and from

Table 1
Number of lactations, cows and mean parity (standard deviation in parentheses) for both breeds[1] available for the present study.

Breed	Lactations	No. of cows	Parity
HF	17,434	10,699	3.12 (1.941)
JFX	10,517	6,199	3.00 (1.909)

[1] Breed: HF = Holstein-Friesian where ≥75% of the breed proportion was Holstein-Friesian; JFX = Jersey × Holstein-Friesian crossbreds where ≥25% of the breed proportion was Jersey.

Table 2
The mean and standard deviation (SD) of Economic Breeding Index (EBI), EBI sub-indices, and predicted transmitting ability (PTA) for milk production traits for both breeds[1].

	HF		JFX	
Traits	Mean	SD	Mean	SD
EBI €	131	44.1	132	32.8
Sub-index (€)				
Milk	36	20.2	46	17.8
Fertility	61	29.2	41	22.8
Beef	-13	6.8	-29	7.0
Maintenance	13	9.6	37	9.6
PTA (kg)				
Milk yield	-3.3	51.17	-66.7	55.80
Fat yield	3.7	2.32	5.1	1.91
Protein yield	2.0	1.65	1.6	1.68

[1] Breed: HF = Holstein-Friesian where ≥75% of the breed proportion was Holstein-Friesian; JFX = Holstein Friesian × Jersey crossbreds where ≥25% of the breed proportion was Jersey.

that calculated total days in milk (DIM), parity and breed. Parity structure was approximately 26, 21, 17, 14 and 22% for parities 1, 2, 3, 4 and ≥5, respectively. The mean calving date of all animals was 19 February, and 24 February for 2016 and 2017, respectively, and 22 February for both, 2018 and 2019. To avoid the influence of own animal performance on its genetic evaluation, EBI was re-calculated for each animal as the parental average EBI obtained from the 2016 national genetic evaluation (i.e. prior to data collection). All cows across the defined breeds were above the top 25% EBI of herds in Ireland with an average EBI of €130 (ICBF, 2019). The mean and standard deviation for the parental average EBI, the sub-indexes and the predicted transmitting ability (**PTA**) are presented in Table 2.

2.2. *Bodyweight, milk solids production, and production efficiency*

Individual cow BW were recorded once per cow in mid-lactation (June to August) for each herd upon exit from the milking parlor by two trained research technicians using a portable electronic scale (Tru-Test Limited, Auckland, New Zealand). The MS production was calculated as the sum of the 305-day fat plus protein production (kg). Measures of production efficiency were based on the net energy system (Faverdin et al., 2011), where 1 Unité Fourragère Lait (**UFL**) is defined as the net energy content of 1 kg of standard barley which is equivalent to 1,700 kcal. Firstly, milk solids production per kg BW (**MSperBW**) in this study was calculated by dividing the 305-day MS production by the mid-lactation BW (kg MS/ kg BW). Secondly, the total energy requirement per kg of MS produced (**ENperMS**) of animals was calculated as total net energy (UFL) requirements (for maintenance (through BW), growth (up to third lactation) and milk production) divided by the total MS production (total UFL/ kg MS). The following equations were used to determine the animals' net energy requirement (**EN**) for maintenance, growth and milk production (INRA, 2010):

ENmaintenance (UFL) = (0.041 * $BW^{0.75}$ (kg) * 1.1) * 365 (days)

ENgrowth (UFL) = (-1.36 + 0.0058 * BW (kg) + 2.16 * BW gain (kg) / 365) * BW gain (kg)

ENmilk (UFL) = 305-day milk yield (kg) * [0.44 + 0.0055 * (fat content (g/kg) - 40) + 0.0033 * (protein content (g/kg) – 31)]

Where BW records were available for the same animals from consecutive years, the animal's own BW gain between parities was calculated. For this, 7250 records were available for the same animals in parity 1 and 2; 4,944 records were available from these animals in parity 3 and 4062 in parity 4. For growing animals with missing BW gain values, a subset population within breed was created and the BW relationship between consecutive lactations from the records where BW gain was available, was calculated.

Additionally, the proportion of energy requirement for milk production from the total energy requirement can be calculated as:

ENmilk% (%) = ENmilk/ ENtotal

While assuming similar maintenance and growth, the energy requirement to produce 1 kg of MS is calculated as:

ENmilk/ kg MS (UFL/ kg MS) = ENmilk/ 305-day MS yield

2.3. *Data edits*

Data edits were applied to remove records of animals weighed at less than 750 days of age. Only records from animals weighed between 60 and 200 days in milk were retained to minimize the impact of changing post-calving body energy status on BW (De Vries and Veerkamp, 2000; Berry et al., 2006). Any individual BW or milk performance traits that exceeded 3 SDs from their respective mean values were considered outliers and were removed. The final dataset comprised 27,951 lactations from 16,898 HF and JFX cows across 80 commercial herds.

2.4. *Statistical analysis*

Stage of lactation at weighing was stratified into 5 classes (≤ 100, 100 to 119, 120 to 139, 140 to 159, and ≥ 160 days in milk at weighing (**DIMw**) and parity was defined as 1, 2, 3, 4 or ≥ 5. Based on the overall parental average EBI, three EBI groups were formed as low EBI (< €100), average EBI (€100 - €149) or high EBI (≥ €150). Animals were also divided into four equally sized quartiles based on their ranking for MSperBW within the 2 breeds HF and JFX (quartile 1 including the least efficient bottom 25% and quartile 4 containing the most efficient top 25% animals).

Table 3
Effect of breed[1] on milk solids (MS) production, mid-lactation bodyweight (BW) and production efficiency parameters.

	Breed		Significance	
	HF	JFX	s.e.	*P*-value
MS production (kg)	503	508	5.76	< 0.001
BW (kg)	544	502	2.35	< 0.001
MSperBW (kg MS/ kg BW)	0.92	1.01	0.01	< 0.001
ENperMS (total UFL[2]/ kg MS)	9.83	9.49	0.043	< 0.001
ENmilk%[3] (%)	60.92	62.10	0.250	< 0.001
ENmilk/ kg MS[4] (UFL/ kg MS)	5.96	5.90	0.004	< 0.001

[1] Breed: HF = Holstein-Friesian where ≥ 75% of the breed proportion was Holstein-Friesian; JFX = Jersey × Holstein-Friesian crossbreds where ≥25% of the breed proportion was Jersey.

[2] UFL: Unité Fourragère Lait (the net energy content of 1 kg of standard barley which is the equivalent to 1700 kcal; Faverdin et al., 2011).

[3] ENmilk% = percentage of total energy requirement dedicated to milk.

[4] ENmilk/ kg MS = energy requirement for milk per kg MS produced.

Regression coefficients were estimated using the following mixed models equations in PROC MIXED (SAS Institute, 3005);

$$Y_{ijklmno} = \mu + Yr_i + B_j + EBI_k + H_l + P_m + L_n + \left(B_j \times P_m\right) + SI_o + e_{ijklmno}$$

where $Y_{ijklmno}$ is the response of the animal in year *i*, of breed *j*, in EBI group *k*, in herd *l*, in parity *m*, at stage of lactation *n*, with sub-index *o;* μ= mean; Yr_i = year ($i = 1$ to 4); B_j = breed (j = HF or JFX); EBI_k = EBI group (k = low, average or high); H_l = herd ($l = 1$ to 80); P_m = parity ($m = 1$ to 5); L_n = stage of lactation ($n = 1$ to 5); $B_j \times P_m$ = interaction between breed and parity; SI_o = respective sub-index (Milk SI or Maint SI, which were both centered within breed and EBI group) and e_{ijkmno} the residual term error. Where the dependent variable (Y) was MS production, the model was adjusted to include Milk SI; where the dependent variable was BW, the model was adjusted to include Maint SI; where the dependent variable (Y) was MSperBW or ENperMS, the model was adjusted and included both, Milk SI and Maint SI. Herd was included as a random effect. Year was fitted as a repeated measure to account for several lactations from individual animals; a first-order autoregressive covariance structure with homogeneous variances assumed among records, provided the best fit to the data. Non-contributing interactions were excluded from the model by backward elimination. Multicollinearity was monitored through the variance inflation factor (VIF), with a VIF of > 10 indicating multi-collinearity.

Repeatability of MS production, BW, MSperBW and ENperMS was quantified using the model described above but with a compound symmetry covariance structure fitted. The proportion of total variance due to measurement replication was calculated as (σ^2_{sample}) / ($\sigma^2_{\text{sample}} + \sigma^2_{\text{error}}$), similar to that described by Berry et al. (2000).

3. Results

3.1. *EBI and milk solids production*

The cows included in this study were of high genetic merit with an average EBI of €130 which is €26 greater than the current national average for herd EBI in Ireland (ICBF, 2019). The mean parental average genetic potential of HF and JFX are presented in Table 2; the animals in this study had higher sub-index (SI) values for milk (+€9), fertility (+€6)

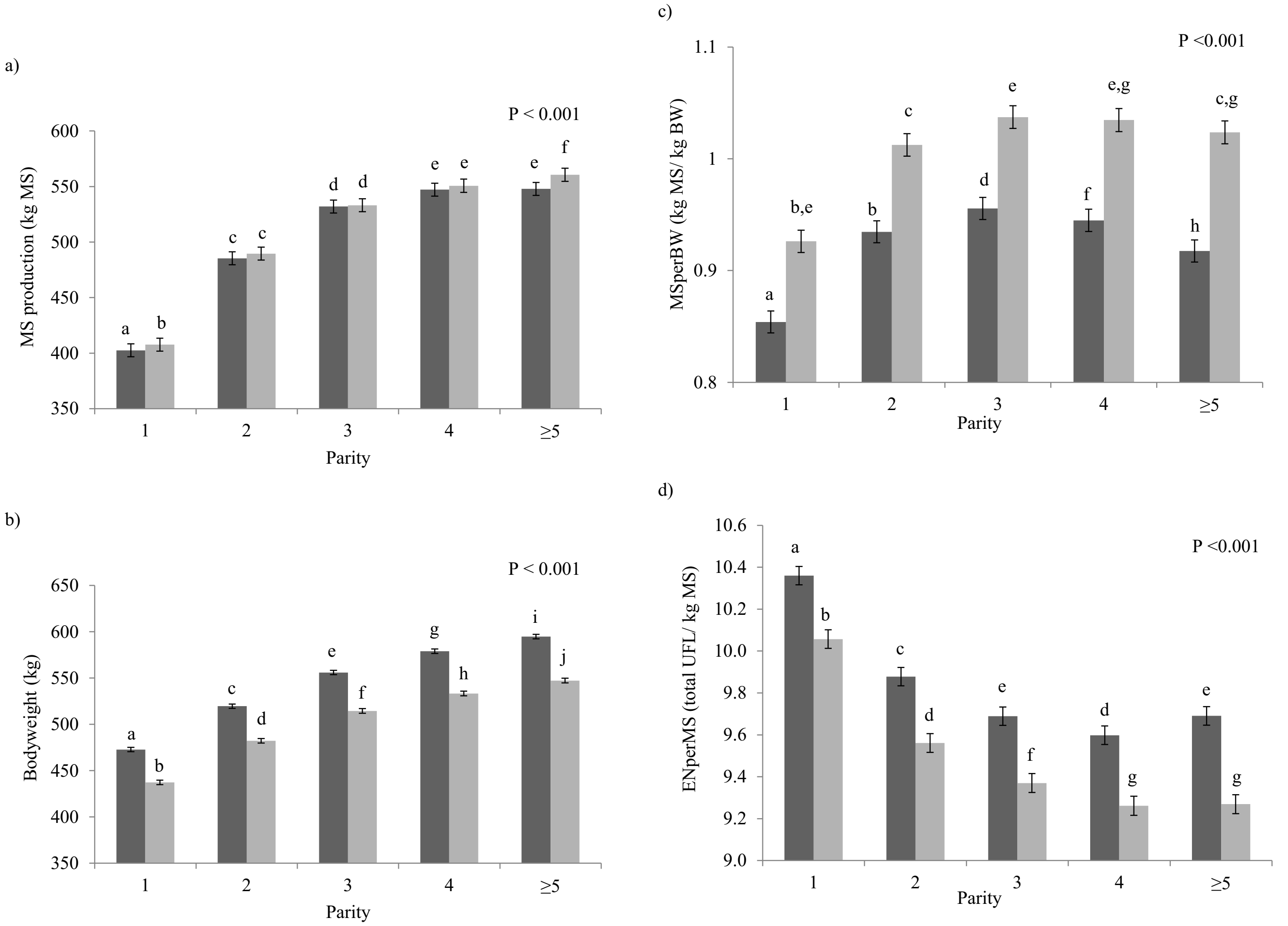

Fig. 1. Effect of parity on (a) milk solids (MS) production, (b) bodyweight, (c) milk solids production per kg bodyweight (MSperBW) and (d) total energy requirement per kg MS produced (ENperMS) for Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian crossbred (light grey) genotypes for parity 1 to 5 (± SE).

and maintenance (+€13) and lower SI values for beef (-€10) than the national average in Ireland (ICBF, 2019). When compared to the HF, the JFX had a higher Milk SI and Maint SI.

A detailed breakdown of the mean, and standard deviation (**SD**) estimates for 305-day lactation milk production, BW and production efficiency parameters for both breeds from the dataset is presented in Table 3. The mean milk yield, MS production, BW, MSperBW and ENperMS for the animals in the study was 5,992 kg, 491 kg, and 522 kg, 0.94 kg MS/ kg BW, and 9.8 total UFL/ kg MS, respectively. Total lactation length (**DIM**) was 286 ± 26 days for both breeds while DIMw averaged 143 ± 26 days. The mean calving date shifted significantly ($P < 0.05$) from February 14 in parity 1 to February 22 for all parities ≥ 2, representing a delay in calving date of 8 days. There was no effect of breed ($P = 0.44$) or breed × parity interaction ($P = 0.27$) on calving date.

Parity had a significant ($P < 0.001$) impact on MS production, peaking at 554 kg MS in parity ≥ 5. Animals in parity 1 and 2 produced less (-128 and -83 kg MS, respectively; $P < 0.001$) compared to animals in parity 3 (533 kg MS). Overall, JFX produced slightly more MS (+5 kg MS/cow/year; $P < 0.001$) compared to HF (503 kg MS/cow/year; Fig. 1a). However, animals from both breeds showed similar yields ($P > 0.05$) in parity 2, 3 and 4 (487, 532 and 549 kg MS, respectively). Peak MS production with 548 kg MS/ cow was achieved for HF animals in parity 4 and ≥ 5, producing + 145 and + 62 and + 15 kg MS/cow/year compared to parity 1, 2 and 3, respectively. There was also a breed × parity interaction ($P < 0.001$) reflecting the greater and more consistent increase in MS production for JFX from parity 1 to 5 (+153 kg MS/cow/year) compared to HF (+145 kg MS/cow/year). With both breed groups, there was a positive relationship observed with each additional €10 of Milk SI corresponding to a 9 kg increase in lactation MS production in mature dairy cows, *i.e.* parity 3 upwards (Fig. 2) while each additional €10 of Milk SI corresponded to a 7 kg increase in lactation MS production when growing and mature animals were considered.

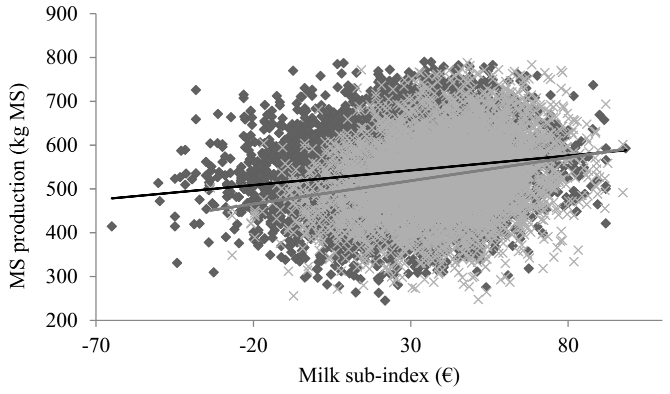

Fig. 2. Relationship between milk sub-index (Milk SI) and milk solids (MS) production for mature (parity ≥ 3) Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian crossbred (grey) genotypes.

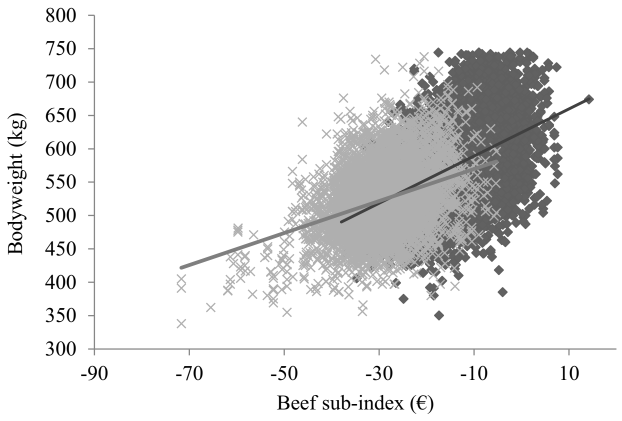

Fig. 3. Relationship between beef sub-index (Beef SI) and mid-lactation bodyweight for mature (parity $\geq$ 3) Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian crossbred (light grey) genotypes.

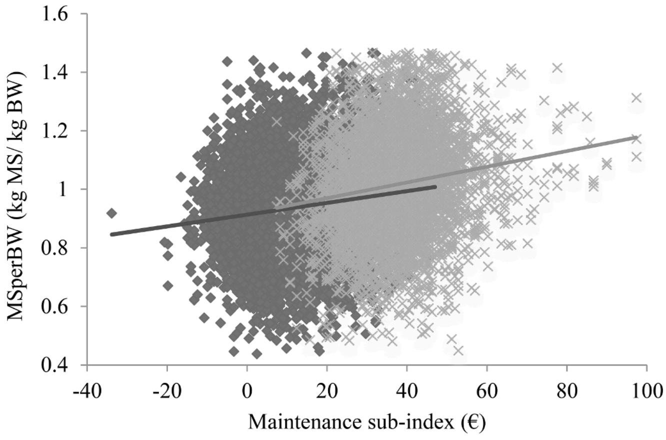

Fig. 4. Relationship between maintenance sub-index (Maint SI) and milk solids production per kg bodyweight (MSperBW) for mature (parity $\geq$ 3) Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian crossbred (light grey) genotypes.

3.2. *Mid-lactation bodyweight*

Overall, animals increased ($P < 0.001$) their mid-lactation BW continuously in each parity. Primi-parous animals from both breeds achieved 85% of the BW of mature animals in parity ≥ 3 (Fig. 1b). After parity 3, animals increased their BW ($P < 0.001$) by +21 and + 36 kg in parity 4 and $\geq$ 5, respectively so that heaviest BW of 594 and 547 kg were recorded in parity $\geq$ 5 for HF and JFX, respectively. Individual cow mid-lactation BW was higher ($P < 0.001$) for HF cows (+42 kg) compared with JFX (502 kg) Similarly, HF animals in parity 3 had a mid-lactation BW of 556 kg which was +83 and +47 kg higher ($P < 0.001$) when compared to parity 1 and 2, respectively, while JFX weighed 77 and 45 kg less in parity 1 and 2, respectively, compared to their mid-lactation BW in parity 3 (514 kg). A moderate positive relationship was observed between Beef SI and mid-lactation BW in dairy cows with each additional €10 increase in Beef SI corresponding to a 27 kg increase for mature animals (Fig. 3) and a 24 kg increase in mid-lactation BW for cows from parity 1–10.

3.3. *Production efficiency*

Overall average MSperBW was 0.94 ± 0.16 kg MS/ kg BW with large variation between farms (0.73 to 1.14 kg MS/ kg BW). Parity had a significant ($P < 0.001$) impact on MSperBW with least efficiency observed in parity 1 (0.89 kg MS/ kg BW), peak MSperBW in parity 3 (1.00 kg MS/ kg BW), and subsequently a slight decrease in MSperBW to 0.99 and 0.97 kg MS/ kg BW in parity 4 and $\geq$ 5, respectively. Moreover, JFX animals had a consistently greater ($P < 0.001$) MSperBW (1.01 kg MS/ kg BW) compared to HF (0.92 kg MS/ kg BW) throughout all parities (Fig. 1c) with a linear increase in MSperBW observed as the proportion of Jersey genes increased. A significant breed × parity interaction ($P < 0.001$) was also observed for MSperBW. Holstein-Friesian cows reached peak MSperBW in parity 3 (0.96 kg MS/ kg BW), yet JFX maintained peak MSperBW in parity 3 and 4 (1.04 kg MS/ kg BW), while also achieving similar ($P = 0.16$) MSperBW in parity 4 and $\geq$ 5 (1.03 kg MS/ kg BW) whereas HF animals reduced to 0.94 and 0.92 kg MS/ kg BW for MSperBW in parity 4 and $\geq$ 5, respectively. A positive relationship was observed between Maint SI and MSperBW with each additional €10 increase in Maint SI corresponding to a 0.03 kg MS/ kg BW increase in MSperBW for all parities and mature animals (Fig. 4).

Furthermore, differences in minimum and maximum ENperMS varying from 8.1 to 15.2 total UFL/ kg MS between animals highlight the significant variation present on farms. In line with the reduction in

Table 4
The least square means, standard error (s.e.) and significance for breed (BR)[1] based on their respective MSperBW efficiency quartile for Economic Breeding Index (EBI), EBI sub-indices (SI), milk solids (MS) production, bodyweight (BW) and production efficiency parameters for mature animals (parity $\geq$3).

Breed	HF					JFX					Significance		
Quartile	1	2	3	4	s.e.	1	2	3	4	s.e.	BR	Quartile	BR × Quartile
Lactation no.	5.1	4.6	4.3	4.0	0.06	4.5	4.4	4.3	4.0	0.07	< 0.001	< 0.001	< 0.001
EBI €	102	106	107	109	2.0	102	104	105	107	2.1	0.06	< 0.001	0.30
Milk SI €	23	27	29	33	0.8	31	34	36	40	0.9	< 0.001	< 0.001	0.20
Fertility SI €	50	48	48	46	1.2	32	31	30	27	1.3	< 0.001	< 0.001	0.556
Beef SI €	-10	-11	-12	-14	0.4	-23	-24	-26	-27	0.4	< 0.001	< 0.001	0.009
Maintenance SI €	10	11	13	15	0.6	29	31	33	35	0.7	< 0.001	< 0.001	0.04
MS production (kg)	469	527	561	609	3.9	472	531	564	613	4.1	< 0.001	< 0.001	0.79
BW (kg)	605	585	570	549	2.9	561	539	523	501	3.0	< 0.001	< 0.001	0.07
MSperBW (kg MS/ kg BW)	0.76	0.89	0.98	1.11	0.002	0.82	0.97	1.07	1.22	0.003	<0.001	-	< 0.001
ENperMS (total UFL[2]/ kg MS)	10.4	9.8	9.4	9.1	0.01	10.1	9.4	9.1	8.8	0.02	< 0.001	< 0.001	0.06
ENmilk%[3] (%)	57.5	61.2	63.3	65.9	0.08	58.4	62.4	64.5	67.2	0.09	< 0.001	< 0.001	< 0.001
ENmilk/ kg MS[4] (UFL/ kg MS)	5.96	5.97	5.96	5.96	0.004	5.88	5.89	5.89	5.89	0.005	< 0.001	< 0.001	0.517

[1] BR = Breed; HF = Holstein-Friesian where $\geq$75% of the breed proportion was Holstein-Friesian; JFX = Jersey × Holstein-Friesian crossbreds where $\geq$25% of the breed proportion was Jersey.

[2] UFL: Unité Fourragère Lait (the net energy content of 1 kg of standard barley which is the equivalent to 1700 kcal; Faverdin et al., 2011).

[3] ENmilk% = percentage of total energy requirement dedicated to milk.

[4] ENmilk/ kg MS = energy requirement for milk per kg MS produced.

Table 5
Regression coefficient and associated standard errors (in parentheses) of milk solids (MS) production, mid-lactation bodyweight (BW) and production efficiency parameters on Economic Breeding Index (EBI), milk (Milk SI), beef (Beef SI) and maintenance (Maint SI) sub-indices where $P < 0.05$.

	EBI (€)	Milk SI (€)	Beef SI (€)	Maint SI (€)
MS production (kg)	0.09 (0.014)	0.72 (0.025)	0.16 (0.065)	-0.25 (0.048)
BW (kg)	-0.04 (0.010)	NS	2.40 (0.050)	-1.97 (0.036)
MSperBW (kg MS/ kg BW)	0.0003 (0.00003)	0.0014 (0.00006)	-0.0044 (0.00019)	0.0032 (0.00010)
ENperMS (total UFL[1]/ kg MS)	-0.0013 (0.00014)	-0.0068 (0.00024)	0.0144 (0.00062)	-0.0104 (0.00046)

[1] UFL: Unité Fourragère Lait (the net energy content of 1 kg of standard barley which is the equivalent to 1700 kcal; Faverdin et al., 2011).

energy requirement for growth between parities, ENperMS decreased ($P < 0.001$) between parity 1 and 4 for both breeds. Unlike MSperBW, ENperMS was lowest in parity 4 (9.4 total UFL/ kg MS). Breed had a significant impact on ENperMS during all parities (Fig. 1d). Overall, JFX animals required fewer total UFL per kg MS produced (-0.34) compared to HF (9.8 total UFL/ kg MS; $P < 0.001$). This equates to +170 additional UFL required for HF animals producing 500 kg MS per cow per lactation, compared to 4750 total UFL for JFX. Moreover, high EBI animals ($\geq$€150) also showed a lower ENperMS (-0.2 total UFL/ kg MS; $P < 0.001$) compared to low EBI cows (<€100; 9.8 total UFL/ kg MS). A significant breed × parity interaction ($P < 0.001$) for ENperMS demonstrates that high EBI JFX animals continue to require less ENperMS from parity 1 to 4 (10.1 to 9.3 total UFL/ kg MS, respectively) and remain similar thereafter (9.3 total UFL/ kg MS), which is in accordance with their energy proportion dedicated to milk production. Whereas HF animals achieved nadir ENperMS in parity 4 (9.6 total UFL/ kg MS) and increased energy requirement to 9.7 total UFL/ kg MS in parity ≥ 5. A negative relationship between Maint SI and ENperMS was also observed with each additional €10 increase in Maint SI corresponding to a 0.11 total UFL/ kg MS reduction in ENperMS for animals from all parities; this is indicative of the reduced energy requirement due to lower BW.

Similarly, JFX dedicated a significantly ($P < 0.001$) greater proportion of their total energy requirement to milk production (ENmilk%; +1.2%) compared to HF animals (60.9%), while HF had a greater proportion of their ENtotal attributed to maintenance (38.5 vs 37.2% for HF and JFX, respectively). In parity 1 animals showed the lowest ENmilk% (-4.5%) before reaching plateau after parity 4 (62.9%). There was a significant breed × parity interaction ($P < 0.001$) indicating that HF lower the ENmilk% after parity 4, whereas JFX maintain it at 63.6% thereafter. Consequently, ENmilk required per kg of MS produced (ENmilk/ kg MS) was lower for JFX (-0.06 UFL/ kg MS; $P < 0.001$) compared to HF (5.96 UFL/ kg MS).

The relationships between genetic potential, breed, and productive efficiency among mature (parity $\geq$3) animals were further evaluated by dividing the data into 4 quartiles based on MSperBW within breed groups (Table 4). For both breed groups, animals in the higher MSperBW quartiles were on average younger and also showed a lower ENperMS as quartiles increase although the overall difference between mature animals from each breed decreased (9.7 and 9.4 total UFL/ kg MS for HF and JFX, respectively). The proportion of total energy requirement contributing to MS production (ENmilk%) also increased significantly ($P < 0.001$) for both breeds to 8.4 and 8.8% for HF and JFX between quartile 1 and 4, respectively. Similarly for energy requirement for milk per kg MS output, where higher quartiles indicate a lower energy requirement. Animals from each quartile had a similar ($P = 0.243$) mean calving date of February 23 and hence similar total lactation length of 282 (SE=0.9) days. While there was no significant impact of breed on overall EBI values ($P = 0.06$), there was a significant effect of breed ($P < 0.001$) on EBI sub-indices due to the increased Milk SI and Maint SI and lower Fertility and Beef SI values of the JFX breed group. In line with the differential in Beef and Maint SI between breeds, JFX had a lower BW ($P < 0.001$) and increased MSperBW ($P < 0.001$) within each quartile compared to HF. Animals in higher MSperBW quartiles had a higher EBI in addition to higher Milk SI and Maint SI, and lower Beef SI values ($P < 0.001$). Overall, the top MSperBW quartile of both, HF and JFX animals, produced more MS (+140 kg MS; $P < 0.001$) and were lighter (-58 kg; $P < 0.001$) than the least efficient quartile. There was a significant breed × quartile interaction ($P < 0.001$) for MSperBW and ENmilk% as the differential between breeds in MSperBW and ENmilk% was greater in higher MSperBW quartiles.

3.4. *Regression coefficient and repeatability*

Overall, EBI was associated with increased MS production and MSperBW, and reduced BW and ENperMS (Fig. 5; Table 5) with each €10 increase in EBI corresponding to an increase of +1 kg MS/cow, a reduction in mid-lactation BW of 0.4 kg, an increase in MSperBW (+0.003 kg MS/ kg BW) and a reduction in ENperMS (-0.01 total UFL/ kg MS). Similarly, for all animals from the study, a €10 increase in Milk SI was also associated with an increase in MS production (+7 kg/cow), MSperBW (+0.01 kg MS/ kg BW), and decline in ENperMS (-0.07 total UFL/ kg MS). In contrast, increasing Beef SI by €10 was associated with an increase in MS production, mid-lactation BW (+1.6 kg MS and +24 kg BW, respectively) and a reduction in production efficiency (-0.04 kg MS/ kg BW for MSperBW, and +0.14 total UFL/ kg MS for ENperMS). Finally, a €10 increase in Maint SI resulted in an increase in MSperBW (+0.03 kg MS/ kg BW) and ENperMS (-0.10 total UFL/ kg MS).

Repeatability estimates were also calculated for MS production, BW, MSperBW and ENperMS. The highest repeatability estimate was obtained for BW at 0.75, while MS yield and ENperMS were lowest (0.33 and 0.35, respectively) and MSperBW was intermediate (0.41). Moreover, repeatability was greater for HF for MS production and MSperBW (0.39 and 0.48, respectively) compared to JFX (0.35 and 0.38, respectively).

4. Discussion

A large array of feed and productive efficiency measures have been developed and studied (Veerkamp, 1998; Berry and Crowley, 2013; Tempelman and Lu, 2020) and selection indices worldwide now include weightings for feed efficiency (Pryce et al., 2014; Cole and Van Raden, 2018). Thus far, reference populations established for the genetic analysis of feed efficiency traits have been primarily limited to research herds with individual animal intake, energy partitioning and performance estimates (Martin et al., 2020). Despite widespread focus and an abundance of proposed measures, there remains no definitive methodology for dairy farmers to select more efficient animals from within their herds to increase the intensity of selection for cow efficiency in the absence of these detailed measures (Coleman et al., 2010; Fischer et al., 2020). This study is the first to evaluate the variability in, and factors influencing, parameters for production efficiency of spring calving pasture-fed dairy cattle using a large sample of commercial dairy farm performance data.

The methodology used to characterize MSperBW (kg MS/ kg BW) in this study is consistent with the characteristics of high efficiency animals in various controlled experiments (Coleman et al., 2010; Grainger and Beauchemin, 2011; Fischer et al., 2020), yet had the added advantage of reflecting the considerable diversity of pasture-based commercial herds and farm systems. Furthermore, values for total UFL intake based on animal intake data reported in a previous study (Prendivillet al., 2009) compare to estimated values for energy requirement from this study in that they indicate that JFX have a lower energy intake per kg MS produced. The results from this study indicate that substantial variation in MSperBW exists between animals not only within herds (between 0.42 and 1.47 kg MS/ kg BW) but also between herds (0.73 to 1.14 kg MS/ kg

BW). Likewise, large variability was evident in terms of ENperMS, which ranged from 9.0 to 10.9 total UFL/ kg MS between herds. Irrespective of breed, highly efficient dairy cattle were characterized by high MS production per cow and a lower mid-lactation BW where animals dedicate a greater proportion of their energy requirement to production, similar to previous studies (Coffey et al., 2018; Fischer et al., 2020).

The impacts of selection using the national breeding objective (EBI) on milk and MS production from this study are in accordance with the recent findings of both O'Sullivan et al. (2019b) within controlled herds and Berry and Ring (2020) using national milk recording data. In fact, within a population of mature (parity $\geq$ 3) high EBI animals, increasing overall parental average EBI resulted in greater 305-day MS production, a minor reduction in mid-lactation BW and a modest improvement in MSperBW and ENperMS (Fig. 5). Similarly, when comparing elite and national average genotypes (differing by >€100 in EBI), O'Sullivan et al. (2019a) and O'Sullivan et al. (2019b) noted a tendency for increased MS production (+8 kg) in favor of genetically elite animals with a lower BW (-13 kg). While the impact of selection on EBI for overall production efficiency is modest, the accuracy and effectiveness of individual sub-indices within EBI to increase MS yield (+7 kg MS per +€10 Milk SI), mid-lactation BW (+24 kg per +€10 Beef SI) and MSperBW (+0.03 kg MS/ kg BW per +€10 Maint SI) was evident within the studied herds (Figs. 2–4). This suggests that selection on the combination of Milk SI and Maint SI within EBI can yield significant improvements in cow production efficiency in both HF and JFX breed groups.

This study is unique in combining individual animal genetics, MS production and BW data to evaluate the variation in, and potential for selection for higher cow efficiency within commercial pasture based dairy systems without resource-intense animal intake data. The results indicate that both MSperBW and ENperMS are genetically controlled and repeatable. In comparison with BW which exhibited a high repeatability (0.75) within the present study, the repeatability of MSperBW (0.41) was greater than ENperMS (0.35) and similar to that reported previously in controlled studies (Prendiville et al., 2011). When the moderate repeatability of MSperBW (and to a lesser extent ENperMS) are considered together with the large variation observed within the population and the significant economic impact on milk revenues, these results suggest that improved productive efficiency by virtue of increased MS production and reduced mid-lactation BW can be accelerated within the EBI breeding goal and as the results clearly demonstrate, increasing overall production efficiency is antagonistically correlated with individual cow BW. However, caution needs to be raised regarding the positive relationship between BW and BCS when differentiating between larger animals with lower BCS and smaller animals with a normal BCS (Köck et al., 2018).

The lactation performance impacts of high MSperBW animals (top 25%), irrespective of breed are considerable and merit further detailed investigation. High MSperBW cows produced +140 kg MS, and without evidence of pasture intake differences impacts due to lower mid-

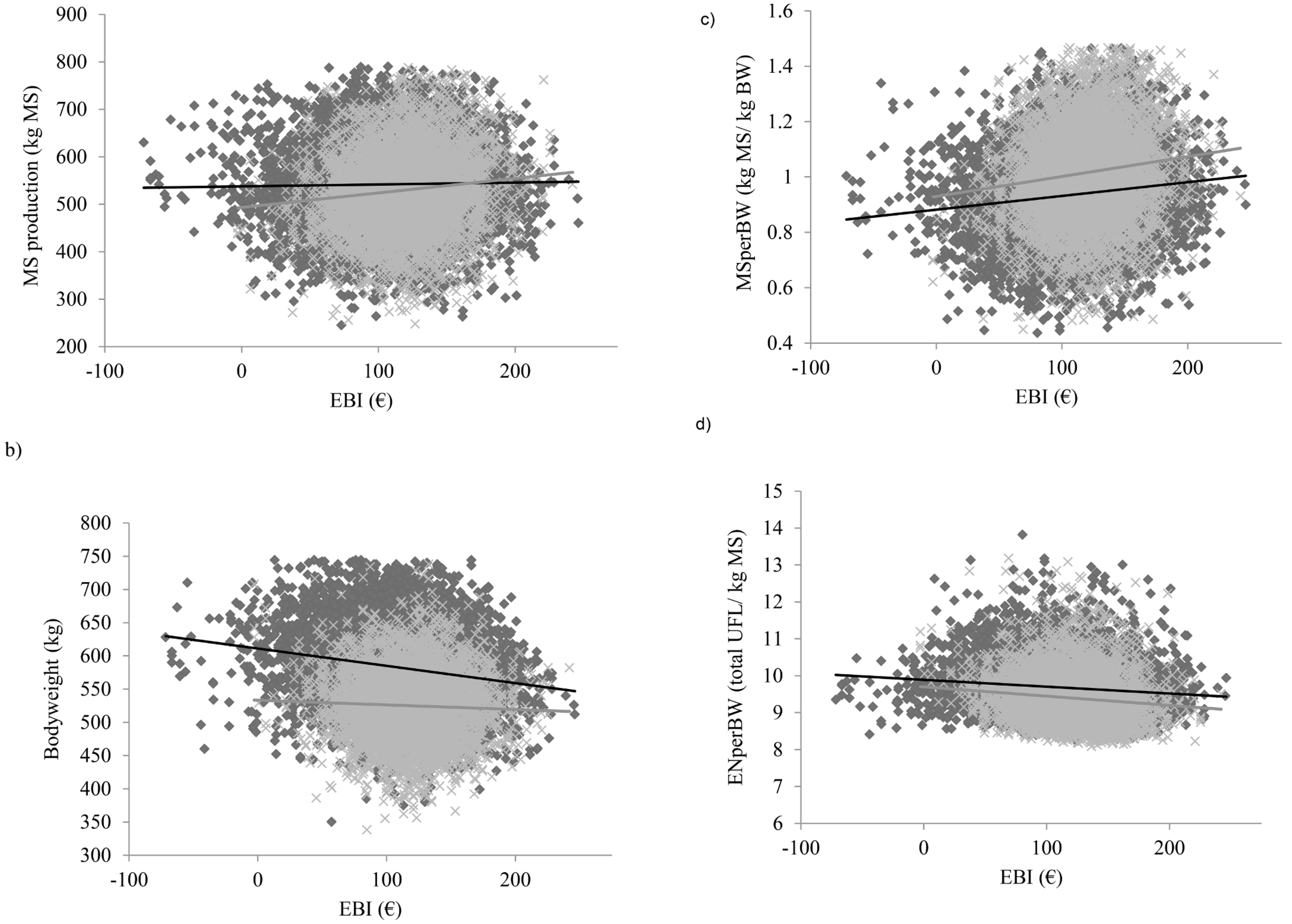

Fig. 5. Relationship between Economic Breeding Index (EBI) and a) milk solids (MS) production, b) bodyweight, c) milk solids production per kg bodyweight (MSperBW) and d) total energy requirement per kg MS produced (ENperMS) for mature (parity $\geq$3) Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian crossbred (light grey) genotypes.

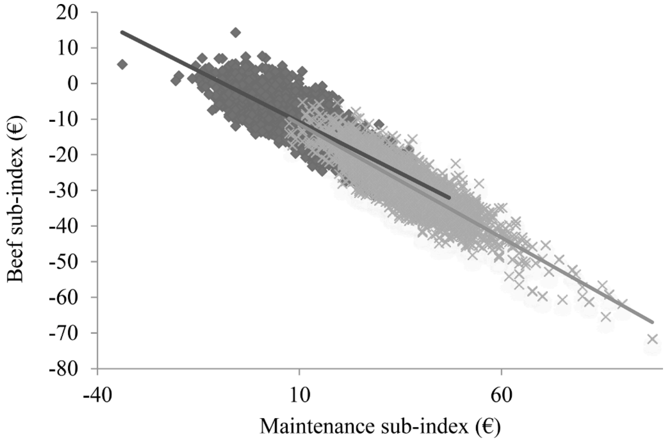

Fig. 6. Relationship between maintenance sub-index (Maint SI) and beef sub-index (Beef SI) for mature (parity ≥3) Holstein-Friesian (dark grey) and Jersey × Holstein-Friesian (light grey) genotypes.

lactation BW (-58 kg), the value of increased milk output at current prices (Ramsbottom et al., 2015; €4.50/ kg MS) increase milk revenue by €630 per cow per lactation (+130%) compared with low MSperBW contemporaries (bottom 25%). Indeed, the evaluation of ENperMS within both breed groups, is characterized by the lower energy requirement per kg MS produced and greater maintenance energy requirements of heavier cows. More recently, Coffey et al. (2017) also observed increased MSperBW among JFX, consistent with the results from this large study where smaller JFX with similar EBI achieved improved MSperBW (+0.09 kg MS/ kg BW) via increased MS production (+5 kg MS), and a lower mid-lactation BW (-42 kg), when compared to larger HF animals. Moreover, Beecher et al. (2015) attributed similar improvements in ENperMS to an increased capacity for forage digestion compared to HF contemporaries.

While the impact of parity on MS production per kg BW and energy requirements has been widely documented in the literature, the presence of significant breed × parity interactions for MSperBW and ENperMS within the current study have not previously received attention. The similarity in mean calving dates for both breeds further accentuates the greater persistency of MSperBW across lactations among JFX animals (reflected by an average MSperBW of 1.01 kg MS/ kg BW in parity 2 and ≥ 5, and 1.04 kg MS/ kg BW in parity 3 and 4, which contrasts starkly with both the lower peak in parity 3 (0.96 kg MS/ kg BW) and greater subsequent reduction in MSperBW (to 0.92 kg MS/ kg BW in parity ≥ 5) for high EBI HF animals. The selection of dairy cattle genotypes capable of improved lifetime performance has been widely acknowledged as the ultimate objective for high productivity and efficient dairy production systems (Cole and VanRaden, 2018; Schuster et al., 2020). To build and strengthen the resilience in the system, Grandl et al. (2019) proposed that the ideal dairy cow should be capable of a high level of productive efficiency coupled with survival within the herd for additional lactations to maximize productivity and minimize the environmental footprint of the overall milk production system. When taken together with the weight of international evidence reporting increased longevity and survival among JFX (Lopez-Villalobos et al., 2000; Buckley et al., 2014), the comparably enhanced production efficiency of mature JFX can be attributed to both high MS production and a superior capacity to increase their MS yield at a similar rate to their BW once matured. On that basis, these results further substantiate the appropriateness of high EBI JFX cattle, complimented by superior fertility performance and improved longevity reported elsewhere (Prendiville et al., 2009; Coffey et al., 2017), to enhance both the productivity and sustainability of pasture-based milk production.

The variability in production efficiency within commercial dairy herds and the overall efficiency of such systems must consider other outcomes including the beef merit of progeny from the dairy herd. Beef SI had a strong negative association with Maint SI (-0.85; Fig. 6) so that attributes such as cullcow value, meat yield and value, age at slaughter and economic returns from dairy as well as dairy beef progeny within pasture-based beef production systems require closer evaluation (Pahmeyer and Britz, 2020; Van Selm et al., 2021). Indeed, the results of the present study must also be considered in the context of the growing interest in improved sexed semen methods (Holden and Butler, 2018) to place increased emphasis on maternal efficiency traits within replacement breeding programs while facilitating increased use of beef semen to increase the beef merit of the non-replacement progeny from the dairy herd (Pahmeyer and Britz, 2020; Van Selm et al., 2021). Further research is also necessary to evaluate more detailed characteristics of contrasting high and low efficiency (MSperBW and ENperMS) animals within controlled experiments in terms of the full lactation profile, DMI, BW and BCS change, fertility, health, longevity and pasture digestion capabilities in early and during various stages of lactation.

5. Conclusion

The results of the present study validate the benefits of high genetic potential within breed, and HF and Jersey crossbreeding programs to increase productive efficiency, both in terms of the MS production per kg BW, and total energy requirement per kg MS produced within intensive grazing systems. Highly efficient dairy cattle were characterized by high MS production and lower mid-lactation BW. Given the large variability in dairy cow production efficiency parameters within herds and the high level of genetic influence, the results of this study suggest that dairy farmers should routinely weigh dairy cattle during mid-lactation. In addition to the milk recording data, these cost-effective measures can help increase the selection intensity for overall production efficiency in future generations and identify the most efficient dairy cows with within the herd to drive animal performance and farm profitability.

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Declaration of Competing Interest

None

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