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Genetic parameters for carcass measurements and age at slaughter in commercial cattle

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ABSTRACT

Genetic parameters were estimated for cold carcass weight (**CCW**), carcass conformation (**CON**), carcass fat class (**FAT**), age at slaughter (**AGE**) and average daily carcass gain (**ADCG**) in 14 common UK breeds of cattle. These included crossbred animals but purebred datasets were also analysed for the most populous sire-breeds. Heritability estimates for beef breeds that were significant ranged from 0.24 to 0.44, 0.12 to 0.35, 0.12 to 0.36, 0.15 to 0.38 and 0.26 to 0.43 for CCW, CON, FAT, AGE and ADCG, respectively. For Holstein-Friesian, a dairy breed, heritability estimates were consistently lower than most beef breeds with estimates of 0.12, 0.13, 0.13, 0.06 and 0.15 for CCW, CON, FAT, AGE and ADCG, respectively. In all breed groups, genetic correlations were positive between CCW, CON and ADCG. In general, genetic correlations were moderate between CCW and CON (0.13 to 0.77), moderate to strong between CCW and ADCG (0.57 to 0.98) and weak or moderate between CON and ADCG (0.12 to 0.82). Genetic correlations for FAT with CCW (-0.20 to -0.42) and CON (-0.16 to -0.52) tended to be negative in the beef breed but were positive in the dairy breed, although not significant between CCW and FAT. For most beef breeds genetic correlations between AGE and carcass traits were not significant with the exceptions of AGE and CCW for Simmental (-0.15) and Salers (-0.24), AGE and CON for Limousin (0.15) and Simmental (0.14) and AGE and FAT from three sire-breeds (-0.17 to -0.35). However, the correlation between AGE and ADCG was negative and moderate to strong in magnitude (-0.23 to -0.67) in all beef breeds as expected since faster-growing animals reach slaughter age earlier. For Holstein-Friesian, all genetic correlations with AGE were negative and moderate to strong. Genetic correlations indicate that selection for increased carcass weight should simultaneously increase growth rate and improve conformation in all breeds and reduce carcass fatness in the majority of beef breeds. The results indicate that there is genetic variation in all five traits suitable for undertaking genetic improvement of carcass traits and age at slaughter; however, there are apparent breed differences. The use of abattoir-derived phenotypes for undertaking genetic improvement is an example where the supply chain can work together to share information to enable the cattle industry to move forward.

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Implication

Merging a combination of data sources, including abattoir data, enabled the genetic analysis of carcass traits on commercial cattle in the United Kingdom. Genetic variation existed for the traits indicating that genetic improvement through the appropriate use of genetic evaluations is achievable. Carcass traits employed in national genetic evaluations should bridge knowledge gaps between pedigree and commercial beef producers and allow them to hit market specifications more efficiently and economically and with less environmental impact.

Introduction

The security of adequate supplies of affordable and safe food is high on the global agenda, together with lessening the impact of food production on the environment (Foresight, 2011). An increasing world population together with income growth has produced an increase in the consumption of animal products and this trend is expected to continue (Delgado et al., 1999). This demand could be met through increased livestock numbers but this would not be without added environmental impact. One strategy for improving global food supply is to increase the efficiency of food production, which in terms of meat production, could be achieved by increasing the output of saleable edible meat per unit input and through reducing associated wastage.

Selective breeding of farmed livestock is one of the most cost-effective ways of improving the animal performance and efficiency of livestock enterprises. In UK beef cattle, the economic benefit was

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estimated to be £4.9 m annually from genetic improvement (Amer et al., 2015). However, realised returns were lower than their expected potential and this could be improved by enhancing genetic evaluations and their greater use by farmers, together with clearer signals between pedigree and commercial sectors. Historically, genetic improvement of beef carcass traits in the United Kingdom has relied on predictor traits (BW, 400-day growth, muscling score and ultrasonically scanned muscle and backfat depths) that are taken on a relatively small number of live pedigree performance recorded selection candidates. Returns from genetic improvement of beef cattle are expected to increase if the estimated breeding values were more closely associated with what farmers were paid for, as genetic correlations between predictor and goal traits are not unity. Genomic selection can further speed up genetic improvement by reducing the generation interval and can be a cost-effective way for selection on traits that occur late in life, or expensive or difficult to measure but success depends upon large numbers of phenotypes in addition to genotypes to predict genomic breeding values.

European Union Regulations (Commission regulation (EEC) 344/91) ensure that UK abattoirs categorise animals into specific age and sex groupings, and provide classifications for conformation, fat and weight to their suppliers. The classes given to the carcass using the EUROP system combined with its weight generally determines the price paid to the farmer. Carcass phenotypes taken from abattoir records are available in large quantities thus could potentially be key target goal traits for many terminal pedigree beef breeders. Genetic evaluations that include both predictor traits on the live animal and carcass data as separate but correlated traits, should improve the accuracy of future genetic evaluations on carcass traits as investigated by Crews Jr et al. (2004).

The British Cattle Movement Service (BCMS) manages the Cattle Tracing System, a database of all bovine animals in Great Britain that has operated since 1998, which captures births, deaths and all other animal movements. From the BCMS database, it is clear that beef production is derived from a plethora of breeds and crosses to suit a variety of markets, production systems and environments. In 2019, 2.6 million birth registrations were recorded from 163 breeds and their crosses, which included 7 breeds with over 100 000 animals registered. Since their establishment, BCMS and equivalent databases in Europe have been considered for purposes other than those for which they were originally developed, such as the genetic improvement of carcass traits (Altarriba et al., 2009).

As the UK beef industry is made up of a number of breeds and crosses, genetic evaluation needs to account for the genetic parameter differences among breeds and crosses. The objective was to estimate genetic parameters for the phenotypes; cold carcass weight (**CCW**), conformation class (**CON**), carcass fat class (**FAT**), age at slaughter (**AGE**) and average daily carcass gain (**ADCG**) and the genetic associations between them for the main breeds that contribute to UK beef production.

Material and methods

Data

Over 8.7 million slaughter records from UK abattoir companies with data from 2001 to 2019 were combined with an extract of data supplied from BCMS with records up to October 2019. The majority of the abattoir data collected was dated from 2008 onwards and in those years represented between 17.2% (in 2008) and 44.1% (in 2017) of the national kill (including calves, prime cattle, cows and bulls) (National Statistics, 2020). Abattoir data included birth date, kill date, breed and category (e.g. heifer, steer, cow and bull), in addition to the carcass measures, and merging with BCMS data-enabled validation or updating of information. British Cattle Movement Service data included the animal's dam, some sire data and all movements from birth to death, thus

allowing the formation of appropriate contemporary groups. A pedigree file was created based on BCMS records and by matching animals to other national data sources and breed societies to provide as much pedigree information as possible.

Traits

The abattoirs supplied data on CCW, CON and FAT. In the United Kingdom, beef carcasses are assessed using the EUROP classification for conformation and a numeric scale for fatness (classes 1–5). The adoption of further class sub-divisions differed among abattoirs in the data received. For analysis, the different conformation and fat scales were transformed to a numerical classification that ranged from 1 to 15 (for conformation 1 and 15 represented the worst and best conformation whereas for fat class 1 and 15 represented the leanest and fattest, respectively, Supplementary Table S1). Age at slaughter and ADCG ($ADCG = CCW/AGE$) were made available through merging abattoir data with BCMS data. However, ADCG was not calculated from birth as we have no BW record. Pesonen and Huuskonen (2015) included BW assumptions in their ADCG calculations for purebred breeds of cattle. However, for our diverse crossbred datasets for simplicity we have followed a similar methodology to Sbarra et al. (2013), omitting BW.

Data edits

Data editing for genetic parameter estimation was carried out separately on individual datasets of the most common sire-breeds of the slaughter generation. These included breed types that are described in the United Kingdom as native beef breeds (Aberdeen Angus, Hereford, Luig, Shorthorn, South Devon and Welsh Black) continental beef breeds (British Blonde, British Blue, Charolais, Limousin, Salers and Simmental), a composite beef breed (Stabiliser) and a dairy breed (Holstein-Friesian). As this is a study on commercial cattle the individual sire-breed datasets included crossbred animals as well as purebreds. Analyses of purebred datasets were carried out on beef sire-breeds where numbers were sufficient.

Birth and finishing herds were extracted from BCMS. An animal may move onto several agricultural holdings during its life. In this study, a finishing herd was defined as the agricultural holding where the animal was located for at least 60 days immediately prior to the sale for slaughter. Two contemporary groupings were formed which were comprised of the birth herd, year and season an animal was born (**BHYS**) and finishing herd, year and season the animal was slaughtered (**FHYS**). Season was defined as three classes (Feb–May; Jun–Sep and Oct–Jan).

Data were edited to include only records for (1) year of slaughter from 2006 to 2019; (2) heifers, steers and young bulls slaughtered between 365 and 1095 days of age with their sires and dams identified; (3) dams at least 450 days of age at first calving; (4) animals where the sire-breed was known and at least 87.5% of one breed; (5) CCW and ADCG within three standard deviations of the mean for their sire-breed, age group (heifers and steers four age groups; young bulls one age group) and category (heifer/steer/young bull) and (6) animals with a maximum of three farm movements. Edits on the number of progeny per sire and contemporary group size were sire-breed specific to allow a manageable, informative and sizeable number of animal records per dataset. The Aberdeen Angus was numerically the most common beef sire-breed and more stringent rules could be applied (at least 50 progeny per sire and at least 10 animals in each BHYS and FHYS group), whereas for the Welsh Black more lenient rules were adopted (at least eight progeny per sire and at least five animals in each birth- and finishing- herd-year). A separate pedigree file was created for each sire-breed consisting of five generations. A summary of the breed-specific edits together with the number of animals in the dataset and corresponding pedigree for each sire-breed is given in Table 1. Descriptive statistics on the studied traits grouped by sire-breed are given in Table 2.

Table 1
Summary of counts, edits and structure for each sire-breed dataset derived from abattoir data on commercial cattle.

Sire-breed	n	n	n	Edit:	Edit:	%	%	%		
	Animals	Sires	Pedigree	Progeny/sire	BHYS, FHYS	Purebred ¹	Dairy dam ²	Heifer	Steer	Young bull
Purebred										
Aberdeen Angus	19283	676	49884	20	5, 5	100	0	29.3	64.3	6.4
Charolais	4136	262	13389	10	5, 5	100	0	28.2	34.6	37.2
Hereford	4050	241	13729	10	5, 5	100	0	28.0	66.7	5.3
Holstein-Friesian	35452	1105	135571	25	5, 5	100	100	4.4	52.5	43.0
Limousin	17761	1231	55787	10	5, 5	100	0	29.8	39.3	30.9
Simmental	14009	765	38892	10	5, 5	100	0	16.0	29.6	54.5
Stabiliser	4796	213	13301	10	5, 5	100	0	17.0	23.5	59.5
Crossbred										
Aberdeen Angus	51717	867	143542	50	10, 10	23.5	9.1	37.1	58.1	4.8
British Blonde	8387	321	27562	10	5, 5	14.4	3.5	41.9	30.0	28.0
British Blue	11303	465	52272	10	5, 5	0.9	49.2	40.6	37.7	21.8
Charolais	47652	1143	147638	30	10, 10	4.6	0.5	45.5	36.6	18.0
Hereford	20976	1092	78630	10	10, 10	25.5	31.8	33.5	63.1	3.4
Limousin	35473	1258	123383	30	10, 10	29.7	7.2	37.5	45.4	17.2
Luing	2601	212	8214	7	5, 5	79.4	0.1	12.9	56.5	30.6
Salers	7693	335	23155	10	5, 5	48.4	0.1	19.1	57.5	23.4
Shorthorn	5046	287	21019	10	5, 5	26.8	0.3	22.2	66.6	11.2
Simmental	27575	982	84373	20	10, 10	39.6	3.4	23.2	38.0	38.8
South Devon	7104	385	23136	10	5, 5	65.6	1.1	25.4	48.2	26.5
Stabiliser	15790	512	39425	10	5, 5	38.9	0.04	22.9	31.0	46.1
Welsh Black	1592	131	5039	7	5, 5	88.3	1.8	19.2	75.6	5.2

BHYS contemporary group birth herd and year, season born; FHYS contemporary group finishing herd and year, season slaughtered.

¹ Percentage of slaughtered animals with at least 87.5% breed composition of the sire-breed.

² Percentage of slaughtered animals that have a dam with at least 87.5% dairy breed composition.

Model

Genetic parameters for CCW, CONF, FAT, AGE and ADCG were estimated using a multitrait animal linear model in ASReml (version Release 3.0; Gilmour et al., 2009). Significance of fixed effects was initially tested using the statistical package SAS (version 9.2; SAS Institute Inc., Cary, NC) to aid the construction of appropriate statistical models. In the literature, it is common for carcase traits to be adjusted with a (co)variable in the model such as weight or age. Employing a multitrait model, however, would make use of phenotypic and genetic correlations between the traits, which means that adjustments using (co)variables would not be necessary. In matrix form the multitrait model is given by Eq. (1):

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 & 0 \\ 0 & 0 & X_3 & 0 & 0 \\ 0 & 0 & 0 & X_4 & 0 \\ 0 & 0 & 0 & 0 & X_5 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 & 0 \\ 0 & 0 & Z_3 & 0 & 0 \\ 0 & 0 & 0 & Z_4 & 0 \\ 0 & 0 & 0 & 0 & Z_5 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix} \tag{1}$$

Table 2
Summary of trait means (and standard deviations in parenthesis) for CCW, CON, FAT, AGE and ADCG grouped by sire-breed group derived from abattoir data on commercial cattle.

Sire-breed	Breed type	Trait mean (SD)					n
		CCW (kg)	CON (1-15)	FAT (1-15)	AGE (d)	ADCG (kg/d)	
Purebred							
Aberdeen Angus	Native	313.2 (40.91)	7.2 (1.24)	10.2 (1.45)	678.6 (122.51)	0.48 (0.11)	19283
Charolais	Continental	381.1 (51.52)	9.8 (1.61)	7.6 (2.02)	631.8 (170.56)	0.65 (0.19)	4136
Hereford	Native	304.2 (36.24)	6.6 (1.06)	10.4 (1.40)	706.1 (125.27)	0.45 (0.10)	4050
Holstein-Friesian	Dairy	308.0 (41.95)	4.1 (1.01)	7.7 (2.01)	627.4 (186.41)	0.52 (0.124)	35452
Limousin	Continental	380.7 (46.77)	11.0 (1.62)	7.6 (2.09)	634.4 (153.63)	0.64 (0.18)	17761
Simmental	Continental	373.2 (44.27)	9.5 (1.43)	8.5 (1.78)	548.5 (145.62)	0.73 (0.19)	14009
Stabiliser	Composite	339.7 (39.74)	8.4 (1.35)	9.2 (1.72)	529.6 (151.54)	0.69 (0.20)	4796
Crossbred							
Aberdeen Angus	Native	316.0 (41.19)	7.2 (1.35)	10.2 (1.38)	668.4 (120.68)	0.49 (0.118)	51717
British Blonde	Continental	368.2 (48.60)	9.6 (2.00)	7.8 (2.20)	624.5 (154.70)	0.63 (0.181)	8387
British Blue	Continental	357.2 (43.25)	8.9 (1.96)	8.1 (2.09)	676.9 (162.04)	0.56 (0.166)	11303
Charolais	Continental	365.4 (46.59)	9.1 (1.40)	9.2 (1.72)	617.0 (131.25)	0.62 (0.16)	47652
Hereford	Native	314.4 (39.58)	6.6 (1.17)	10.4 (1.43)	716.9 (128.61)	0.45 (0.098)	20976
Limousin	Continental	360.7 (49.04)	9.6 (1.79)	8.7 (1.97)	660.5 (145.0)	0.58 (0.162)	35473
Luing	Native	332.4 (40.15)	7.8 (1.15)	10.0 (1.58)	630 (152.4)	0.56 (0.148)	3017
Salers	Continental	354.4 (42.24)	8.1 (1.18)	8.9 (1.75)	672.6 (148.94)	0.55 (0.144)	7693
Simmental	Continental	357.6 (47.17)	9.0 (1.47)	8.8 (1.77)	590.4 (152.53)	0.65 (0.197)	27575
Stabiliser	Composite	332.7 (43.57)	8.2 (1.42)	9.3 (1.71)	556.9 (146.60)	0.64 (0.195)	15790
Shorthorn	Native	330.4 (44.04)	7.5 (1.29)	10.1 (1.49)	673.6 (136.16)	0.51 (0.137)	5046
South Devon	Native	345.6 (42.53)	8.1 (1.50)	8.6 (1.94)	662.0 (162.86)	0.56 (0.172)	7104
Welsh Black	Native	315.1 (37.23)	7.2 (1.19)	8.6 (1.97)	816.4 (127.84)	0.40 (0.082)	1592

CCW = cold carcase weight; CON = carcase conformation class; FAT = carcase fat class; AGE = age at slaughter; ADCG = average daily carcase gain.

where y is the vector for observations (CCW, CONF, FAT, AGE and ADCG); b is the vector with fixed effects for the purebred analysis consisting of category (heifer, steer and young bull), dam age class (≥ 450 d and < 1095 d; ≥ 1095 d and < 2190 d; ≥ 2190 d and < 3285 d and ≥ 3285 d), abattoir site, the contemporary group of FHYS, the contemporary group of BHYS; u is the vector of random effect of the animal; X and Z are the incidence matrices for fixed effects and random effects, respectively and e is the vector of residual effects. For the analyses that included crossbred animals, additional breed effects consisted of dam breed group (breed group given in BCMS), percentage of dairy in dam breed and the covariates heterosis and recombination. Many breeds were represented within the crossbred datasets with numerous dam breeds present. It was thought not to be practical in this study to calculate heterosis and recombination coefficients between all possible breed combinations, therefore the individual breeds were classified into four breed types; dairy, native beef, continental beef and other breeds. The heterosis/recombination coefficients (in this case six different coefficients for each animal) were included in the model as covariates. Heterosis and recombination coefficients were calculated from the breed type proportions of the animal's sire and dam and are shown by [formulae 2 and 3](#), respectively:

$$\text{heterosis}_{ij} = \frac{(\text{sire}_i * \text{dam}_j) + (\text{sire}_j * \text{dam}_i)}{100} \quad (2)$$

$$\text{recombination}_{ij} = \frac{(\text{sire}_i * \text{sire}_j) + (\text{dam}_i * \text{dam}_j)}{100} \quad (3)$$

where i and j correspond to two different breed types.

To justify whether age should be included as a covariate or analysed as a trait itself, multitrait models with three (CCW, CON and FAT) and five traits were explored, including linear and quadratic regression on AGE of the other traits.

Results

Descriptive statistics

For beef sire-breeds, the results focus on the larger datasets, including crossbreds that better reflect the commercial environment, but purebred results are given for some breeds for comparison. Trait means between sire-breeds ranged from 308.3 to 368.2 kg, 4.1 to 9.6, 7.7 to 10.4, 556.9 to 816.4 days, and 0.40 to 0.65 kg/day for CCW, CON, FAT, AGE and ADCG, respectively. Of the beef breeds the continental sire-breeds, such as British Blonde, Charolais and Limousin, had the

heaviest carcasses whilst the native sire-breeds, Welsh Black, Aberdeen Angus and Hereford, had the lightest carcasses at slaughter. The dairy breed, Holstein-Friesian, had the lightest mean carcass weight overall. The most highly conformed carcasses were obtained from continental sire-breeds British Blonde, Charolais and Limousin whereas the least conformed were from Holstein-Friesian and Hereford sire-breeds. The native sire-breeds Hereford, Aberdeen Angus, Shorthorn and Luing had the fattest carcasses whilst the Holstein-Friesian had the least fat followed by beef sire-breeds British Blonde and British Blue. Mean AGE was earliest in the Stabiliser and latest in the Welsh Black and Hereford sire-breeds. Average daily carcass gain was highest in Stabiliser, Simmental and British Blonde and lowest in the Welsh Black, Hereford and Aberdeen Angus sire-breeds.

Genetic parameter estimates

Estimates of heritability are given in [Table 3](#) (and Supplementary Table S2 for purebred datasets). Significant heritability estimates for the beef sire-breed groups ranged from 0.24 to 0.44, 0.12 to 0.35, 0.12 to 0.36, 0.15 to 0.38 and 0.26 to 0.43 for CCW, CON, FAT, AGE and ADCG, respectively. Heritability estimates from Holstein-Friesian tended to be lower than most beef sire-breeds with estimates of 0.12, 0.13, 0.13, 0.06 and 0.15 for CCW, CON, FAT, AGE and ADCG, respectively. The heritability estimates of carcass traits CCW, CON and FAT were similar between the trivariate model (with age fitted as a covariate) and the five-trait model (with age regarded as a trait). For CCW, the additive genetic variance tends to be lower and the residual variance higher when age as a covariate is replaced as a trait in the model, which in some cases lowered the heritability slightly in the five-trait analysis (Supplementary Table S3), whereas CON and FAT, appeared unchanged. Results from the smaller datasets, such as Welsh Black and Luing, should be treated with caution as standard errors were high.

A summary of the genetic correlations is presented in [Table 4](#) for the seven sire-breeds with the largest datasets (results from the smaller sire-breed datasets are given in Supplementary Table S4). Genetic correlations were positive and in general, moderate between CCW and CON with significant correlations ranging from 0.15 (Aberdeen Angus) to 0.77 (Luing). In beef sire-breeds, genetic correlations between CCW and FAT tended to be negative and ranged from -0.20 (Hereford and Stabiliser) to -0.42 (Charolais) whereas for Holstein-Friesian it was positive although not significant. Correlations between CCW and AGE were significant in three breeds (Simmental, Salers and Holstein-Friesian) and ranged from -0.15 to -0.38 that indicates animals with heavier carcasses are slaughtered at a younger age. For all breeds, in general genetic correlations between CCW and ADCG were high

Table 3 Estimates of heritability for slaughter traits¹ (with standard errors in parenthesis) for crossbred commercial cattle sire-breed datasets from three-trait and five-trait multivariate models.

Sire-breed	Heritability h^2 (SE)							
	Three-trait model			Five-trait model				
	CCW	CON	FAT	CCW	CON	FAT	AGE	ADCG
Aberdeen Angus	0.32 (0.017)	0.24 (0.016)	0.28 (0.017)	0.31 (0.016)	0.24 (0.016)	0.28 (0.017)	0.19 (0.015)	0.37 (0.018)
British Blonde	0.25 (0.040)	0.17 (0.035)	0.27 (0.039)	0.24 (0.038)	0.17 (0.034)	0.27 (0.039)	0.27 (0.039)	0.30 (0.041)
British Blue	0.31 (0.044)	0.26 (0.043)	0.27 (0.041)	0.30 (0.044)	0.27 (0.043)	0.27 (0.041)	0.26 (0.041)	0.34 (0.044)
Charolais	0.26 (0.016)	0.20 (0.014)	0.24 (0.015)	0.25 (0.016)	0.20 (0.015)	0.24 (0.016)	0.28 (0.018)	0.31 (0.018)
Hereford	0.42 (0.029)	0.21 (0.025)	0.29 (0.028)	0.39 (0.029)	0.21 (0.025)	0.28 (0.028)	0.30 (0.028)	0.43 (0.029)
Holstein-Friesian	0.13 (0.015)	0.13 (0.015)	0.13 (0.015)	0.12 (0.014)	0.13 (0.015)	0.13 (0.015)	0.06 (0.011)	0.15 (0.016)
Limousin	0.24 (0.020)	0.28 (0.021)	0.33 (0.021)	0.24 (0.019)	0.29 (0.021)	0.33 (0.021)	0.22 (0.019)	0.26 (0.020)
Luing	0.33 (0.073)	0.16 (0.057)	0.36 (0.078)	0.33 (0.069)	0.17 (0.056)	0.36 (0.077)	0.06 (0.045)	0.43 (0.077)
Salers	0.33 (0.044)	0.12 (0.033)	0.24 (0.042)	0.31 (0.043)	0.12 (0.033)	0.24 (0.041)	0.23 (0.039)	0.40 (0.047)
Shorthorn	0.37 (0.063)	0.22 (0.055)	0.12 (0.045)	0.33 (0.061)	0.22 (0.055)	0.12 (0.044)	0.38 (0.066)	0.41 (0.065)
Simmental	0.30 (0.022)	0.20 (0.019)	0.30 (0.021)	0.27 (0.021)	0.20 (0.019)	0.30 (0.021)	0.23 (0.021)	0.33 (0.022)
South Devon	0.45 (0.051)	0.27 (0.044)	0.30 (0.045)	0.44 (0.051)	0.27 (0.044)	0.30 (0.045)	0.31 (0.048)	0.42 (0.049)
Stabiliser	0.34 (0.028)	0.35 (0.028)	0.34 (0.027)	0.32 (0.027)	0.35 (0.028)	0.34 (0.027)	0.15 (0.021)	0.34 (0.028)
Welsh Black	0.25 (0.106)	0.10 (0.085)	0.06 (0.071)	0.26 (0.103)	0.11 (0.085)	0.05 (0.071)	0.32 (0.100)	0.31 (0.109)

¹ CCW = cold carcass weight; CON = carcass conformation class; FAT = carcass fat class; AGE = age at slaughter; ADCG = average daily carcass gain.

Table 4
Genetic correlations between slaughter traits in continental beef, native beef, composite beef and dairy sire-breed groups.

Trait ¹	Genetic correlations r_g (SE)						
	Limousin	Charolais	Simmental	Aberdeen angus	Hereford	Stabiliser	Holstein-Friesian
CCW-CON	0.24 (0.054)	0.34 (0.046)	0.13 (0.063)	0.15 (0.044)	0.21 (0.069)	0.26 (0.060)	0.33 (0.076)
CCW-FAT	-0.24 (0.055)	-0.42 (0.049)	0.01 (0.057)	-0.26 (0.044)	-0.20 (0.070)	-0.20 (0.065)	0.06 (0.084)
CCW-AGE	0.07 (0.062)	-0.01 (0.049)	-0.15 (0.064)	-0.09 (0.050)	0.00 (0.065)	-0.07 (0.085)	-0.38 (0.108)
CCW-ADCG	0.78 (0.024)	0.80 (0.018)	0.85 (0.018)	0.89 (0.011)	0.88 (0.015)	0.88 (0.017)	0.92 (0.018)
CON-FAT	-0.52 (0.044)	-0.42 (0.049)	-0.30 (0.061)	-0.16 (0.048)	-0.11 (0.083)	-0.26 (0.061)	0.35 (0.075)
CON-AGE	0.15 (0.059)	0.09 (0.052)	0.14 (0.069)	0.03 (0.055)	-0.06 (0.080)	0.04 (0.082)	-0.39 (0.100)
CON-ADCG	0.12 (0.056)	0.20 (0.047)	0.08 (0.061)	0.13 (0.044)	0.23 (0.067)	0.21 (0.060)	0.40 (0.070)
FAT-AGE	-0.07 (0.057)	-0.09 (0.050)	-0.05 (0.061)	-0.07 (0.052)	-0.07 (0.073)	-0.17 (0.081)	-0.44 (0.099)
FAT-ADCG	-0.13 (0.054)	-0.25 (0.047)	0.01 (0.054)	-0.19 (0.043)	-0.14 (0.066)	-0.06 (0.064)	0.24 (0.075)
AGE-ADCG	-0.50 (0.047)	-0.57 (0.032)	-0.55 (0.044)	-0.48 (0.039)	-0.43 (0.052)	-0.44 (0.068)	-0.67 (0.070)

¹ CCW = cold carcass weight; CON = carcass conformation class; FAT = carcass fat class; AGE = age at slaughter; ADCG = average daily carcass gain.

and positive, ranging from 0.57 to 0.98 which indicates faster-growing animals have a higher carcass weight. In beef breeds, all significant genetic correlations between CON and FAT were negative and ranged from -0.16 (Aberdeen Angus) to -0.52 (Limousin) whereas it was positive for Holstein-Friesian (0.35 ± 0.075). For the majority of sire-breeds, the genetic correlation between CON and AGE was low and not significant, with the exception of the Limousin (0.15 ± 0.059) and Simmental (0.14 ± 0.069). In all breeds, genetic correlations between CON and ADCG were positive and ranged from 0.12 (Aberdeen Angus) to 0.82 (Luing), indicating that faster-growing animals had better carcass conformation. The genetic correlation between FAT and AGE was negative (-0.17 to -0.44) but was only significant for four sire-breeds, namely British Blue, Holstein-Friesian, Salers and Stabiliser. Genetic correlations between FAT and ADCG were significant in four beef breeds and were negative ranging from -0.13 to -0.25. However, the genetic correlation between FAT and ADCG was positive for Holstein-Friesian (0.24 ± 0.075). In all breeds, the genetic correlation between AGE and ADCG was negative and was moderate to high ranging from -0.23 (South Devon) to -0.67 (British Blonde and Holstein-Friesian) indicating that animals that grow faster are slaughtered at younger ages.

Discussion

Genetic parameter estimation was carried out for sire-breeds that had a sizeable dataset after data edits, determined by breed population size in the abattoir data as well as the level of known sire identity. Data structures studied may not reflect the national herd entirely, as only slaughter progeny with a known sire were selected and only a sample of abattoirs supplied data. The pedigree for the majority of commercial slaughter animals relies upon their sire recorded in BCMS. However, recording of the sire is not compulsory; therefore data bias may exist if a finisher is part of a payment scheme based on sire or breed. The level of sire recording (or lack of) in BCMS was reported earlier (Pritchard et al., 2012) with findings that native British breeds tended to have a greater percentage of recorded sires. Still, recording of sire appears to be improving each year and sometimes this can be further enhanced via a combined pedigree with added information from other sources (breed societies, pedigree information collected for beef and dairy genetic evaluations) in addition to BCMS. In 2018, 32% of slaughter animals aged 12–36 months had sire recorded in BCMS, which was further enhanced to 43% using a combined pedigree. For births registered in 2018, on the breeds studied, sire recording was highest in the Stabiliser (80%) whereas it was lowest in Holstein-Friesian (6%) and British Blue (10%). However, sire records increased to 58% and 36% for Holstein-Friesian and British Blue, respectively, via the combined pedigree.

This study partly reveals the diverse nature of the UK beef industry, by including sire-breeds described as lowland and upland, native and continental, bred to suit intensive to extensive environments, some of

which are kept mainly to produce purebreds whilst others are used to produce crossbreds (either beef-beef or beef-dairy crossbreds). Therefore, when comparing results the data structure and production system the breed is mainly used is important to consider. Sire breeds that are largely bred to dairy cows to produce crossbred calves are likely to have progeny with lower conformation scores compared to those generally bred with cows of beef breeds. For instance, the British Blue sire-breed dataset had the highest percentage of slaughter progeny that came from dairy dams (49%), followed by Hereford (32%). Also, in some breeds, rearing bulls is more common, and these are generally sold before 16 months of age due to price incentives. The Holstein-Friesian had the highest percentage of bulls (47%) and the lowest percentage of heifers (3%) within its dataset since dairy females are bred as replacements for the dairy herd. Of the beef sire-breeds, the Stabiliser followed by the Simmental had the highest percentage of bulls within their dataset (46% and 39%, respectively) and descriptive statistics reveal these breeds were also among the earliest to slaughter and attaining higher ADCG.

Genetic parameter estimation

The genetic parameters across all five traits are similar in scale and direction in many of the beef breeds and crossbred animals. However, the traits have lower heritability for dairy animals (Holstein-Friesian) and the correlation between traits also differs for dairy versus beef breeds. Genetic parameters were determined using a 5-trait multitrait model so that adjustments such as using age or weight for the traits CCW, CON or FAT would not be required. The consistency of the parameter estimates within the dairy and beef sire-breeds were compared for the carcass traits alone (trivariate) with the results from the five trait multivariate analysis (including AGE and ADCG). The five trait analysis allows for a greater range of future industry implementation as not all animals may have carcass data routinely available for proprietary reasons and therefore inclusion of AGE which can be derived from nationally available data allows for all animals (cross- and purebred) to have at least one of these five important production efficiency traits.

Heritability estimates

The estimates for CCW, CON and FAT were in line with the review by Ríos Utrera and Van Vleck (2004) reporting moderate average heritability estimates from the literature of 0.40, 0.36 and 0.40, respectively, for similar traits. However, it was found in their study that there was a wide range in heritability estimates with estimates for CCW that ranged from low (0.09) to high (0.92) in magnitude and one reason could be due to breed differences. For CCW, our estimates from beef sire-breeds were also within the ranges that Hickey et al. (2007) reported in Ireland with heritability estimates between 0.17 and 0.65 in six beef sire-breeds of dairy crosses. Likewise, Kause et al. (2015) reported heritability estimates for CCW that ranged from 0.39 to 0.51 in purebred Finnish

Hereford, Angus, Limousin, Simmental and Charolais beef breeds and Altarriba et al. (2009) estimated heritability of 0.34 in Spanish Pirenaica yearling beef cattle. In Swedish pure beef breeds, Eriksson et al. (2003) reported heritability estimates for CCW of 0.45, 0.70 and 0.42 in Charolais, Hereford and Simmental breeds, respectively. Our estimates were lower than Eriksson et al. (2003) for the same pure or cross-bred breed groups, which supports estimating country-specific genetic parameters but possibly our study benefits from larger dataset sizes. The results from Eriksson et al. (2003) and Kause et al. (2015) all present slightly higher estimates from the early maturing breeds compared with the later maturing breeds, and our estimates for early maturing breeds also tend to be at the higher end of the heritability range for CCW. In the present study, a lower estimate was obtained from the Holstein-Friesian group (0.12) and other studies have reported heritabilities of similar magnitude in dairy breeds (Parkkonen et al., 2000; Hickey et al., 2007) ranging from 0.06 to 0.18.

Our low and moderate heritability estimates for conformation and fat are in the range of those in the literature using the EUROP system. For conformation class, a number of studies reported estimates between 0.21 and 0.44 for beef breeds (Eriksson et al., 2003; Altarriba et al., 2009; Kause et al., 2015), 0.09–0.36 for beef-dairy crosses (Hickey et al., 2007) and 0.04–0.31 in dairy breeds (Parkkonen et al., 2000; Hickey et al., 2007). In the same studies, estimates of fat class ranged from 0.19 to 0.45 in beef breeds (Eriksson et al., 2003; Altarriba et al., 2009; Kause et al., 2015), 0.15 to 0.40 for dairy-beef crosses (Hickey et al., 2007) and 0.08 to 0.21 in dairy breeds (Parkkonen et al., 2000; Hickey et al., 2007).

Moderate heritability estimates reported by Sbarra et al., 2013 from 0.27 to 0.42 for ADCG in three breeds of Italian bulls were not dissimilar to our results. Few studies in cattle have reported heritability estimates on ADCG, a function of CCW and AGE. Average daily carcass gain enables the understanding of relationships between the other traits but as a trait on its own, it is deficient in an end-point (such as CCW or AGE). Limited literature also exists on genetic parameter estimates for AGE, which is often included in models as an environmental effect correcting for carcass traits to a common end-point (Ríos Utrera and Van Vleck, 2004) rather than as a trait itself that reflects differences between animals to reach finishing. However, more recently it is being increasingly recognised that AGE is a heritable trait and not merely an environmental factor to correct other traits (Bittante et al., 2011; Sbarra et al., 2013), which is further demonstrated by the present study. It should not be surprising that AGE has a genetic component since it depends on other traits that have been reported to have a genetic component, such as feed intake, feed conversion efficiency and growth (Crowley et al., 2010). Sbarra et al. (2013) studied AGE in bulls of three Italian beef breeds and obtained estimates between 0.28 and 0.39. Our estimates for AGE were wide-ranging depending upon the sire-breed, however, the estimates of Sbarra et al. (2013) are within the range of our estimates. Although, Bittante et al. (2011) investigated the age of calves at sale at a young age rather than for slaughter it also demonstrates that an age-trait is heritable. Similar results were described by Bittante et al. (2011) who reported a biased result and an increased heritability of 9% for their weight trait when age was fitted as a covariate compared to the bivariate model with both weight and age. In this study, CCW had an increased heritability estimate of 0.33 when age was fitted as a covariate compared with 0.32 when age was a correlated trait in the model. Nonetheless, there is likely to be a large managerial aspect to AGE as farmers will adopt different selling strategies according to their specific situation. Farmers will be influenced by factors such as market price fluctuations, farm size, feed type, seasonality, animal health status, veterinary withdrawal periods and TB restrictions. Yet, despite these many managerial factors it is expected that animals sharing a contemporary group on the same farm have similar treatment and are sold in the order they reach finishing.

Genetic correlations

The genetic correlation results indicate that there are differences between sire-breed groups. In general, the genetic correlations between traits obtained from beef sire-breeds followed the same direction (positive/negative) although they may vary in magnitude. However, it is observed that the genetic correlations between some traits behaved differently in the dairy breed (Holstein-Friesian), which tended to be trait combinations with FAT. These differences in genetic correlation for beef and dairy sired animals are not unexpected since breeding goals differ for the two breed types and selection has gone in different directions. As a result of their genetic divergence, beef and dairy cattle breeds display distinct patterns in selected metabolic pathways related to muscling, marbling and milk composition traits. Similarly, these differences between beef and dairy breeds were also reported by Hickey et al. (2007). Kause et al. (2015) also reported differences among beef breeds finding that genetic correlations between conformation and fat were close to zero in Angus, Hereford and Simmental, but negative in Charolais and Limousin breeds. Likewise, in this study, although we report all the genetic correlations between these traits to be negative, the genetic correlations from Hereford and Angus were lower in magnitude (−0.11 to −0.16) in comparison to Charolais and Limousin sire-breeds (−0.42 to −0.52), whereas Simmental was intermediate (−0.30). Although in the United Kingdom, the Simmental is classed as a continental breed the results from these sire-breed analyses show that it does not always act so similar to other continental breeds such as the Limousin and Charolais sire-breeds with genetic correlations lower in magnitude between pairwise combinations of CCW, CON and FAT. In summary, the genetic correlations indicate that selection for increased carcass weight should simultaneously increase growth rate, improve conformation in all breeds and reduce carcass fatness in the majority of beef breeds.

The direction of phenotypic and environmental correlations sometimes differed from the genetic correlations. Both phenotypic and environmental correlations between net weight and fat in all breeds were positive, which indicates heavier carcasses are characterised by increased fatness. However, in beef breeds, the negative genetic correlation implies that animals with greater genetic merit for heavier carcasses tend to have lower genetic merit for fatness cover. Similarly, phenotypic and environmental correlations indicated that older animals at slaughter were characterised by heavier carcasses but the negative genetic correlations indicate that animals with greater genetic merit for heavier carcasses tend to have earlier ages at slaughter (i.e. faster growth rate), which is also supported by the genetic correlations between CCW and ADCG.

Conclusion

Genetic analysis of carcass traits on commercial cattle has been made possible through data supplied from abattoirs, particularly for individual breeds that make up a major part of the cattle population and where sire identity is recorded in national cattle movement data. Genetic variation was apparent in all five traits for undertaking genetic improvement of carcass traits. Thus, these results warrant further investigation on the relationship of carcass traits and other traits of importance in the beef selection index, such as antagonistic effects with maternal production efficiency traits. Breed differences are clear and these differences need to be accounted for in genetic evaluations of carcass traits and warrants further work on heterotic effects between individual breeds. The knowledge gap between pedigree breeders and the commercial beef producer could be lessened via carcass trait evaluations. Pedigree breeders would be given clearer signals on where improvements are needed allowing benefits to flow into the commercial beef sector with cattle that better hit market specifications more efficiently. For the cattle industry to make progress it is vital that the various parts of the food chain work together by sharing information, which in part has been demonstrated in this study.

Supplementary materials

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.animal.2020.100090>.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository given the commercial nature of some of the data.

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Declaration of interest

None.

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