



Heritability and genetic correlation of body weight and Kleiber ratio in Limousin and Charolais beef cattle breeds



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ARTICLE INFO

Article history:

Received 24 June 2021

Revised 23 March 2022

Accepted 25 March 2022

Keywords:

Bayesian inference
Genetic parameters
Growth
Growth efficiency
Metabolic weight

ABSTRACT

Reducing the environmental impact of livestock production is now indispensable and genetic selection can be of great support for this purpose. Measures that can identify high body growth at low maintenance costs in production animals are particularly useful since resources have been increasingly limited. Therefore, the goal of this study was to estimate genetic parameters for BW and Kleiber ratio (**KR**) in 210-day-old and 365-day-old Charolais and Limousin breeds. A database comprising animals born from 1999 to 2018 was used in a multitrait model applying Bayesian inference. The heritability for BW is high in Charolais (0.39 and 0.42 for BW210 and BW365, respectively) and moderate in Limousin (0.22), indicating possible genetic gains for BW in both breeds. The genetic variability of KR should also allow satisfactory genetic gains. In addition, the genetic correlation between BW and KR ranged from low to moderate. Thus, selection over KR should have no effects on BW, showing that high body growth can be obtained without changes in efficiency.

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Implications

This work contributes to the selection and the genetic improvement of feeding efficiency in beef cattle using a tool that disregards the measurement of individual feed intake. This strategy is particularly favourable to large herds or production systems that lack the tools or resources to take individually based measurements. The results show that the genetic variability of the Kleiber ratio is likely to allow satisfactory genetic gains. The selection over Kleiber ratio has no effects on body weight, besides reducing the costs for evaluation of herds.

Introduction

It is now consolidated that the environmental impact of cattle breeding is high but at the same time, meat production is necessary, at least in the short and medium term, to support the world population from a food point of view. In this contrast is therefore placed the need to develop selective models that can produce the

raw material reducing as much as possible the environmental impact of the production system.

Increased body growth associated with reduced feed intake is a target in beef cattle breeding programmes in order to improve the efficiency and profitability of production systems (Archer et al., 2004). Animals with poor feed efficiency not only deficient growth but also produce more carbon dioxide and methane. Thus, the classification of animals according to their efficiency in feed intake represents an important and desirable criterion for farmers. The main limitation for selecting growth and feeding efficiency in beef cattle is the difficulty to measure the individual food intake in many animals since most indexes require individual measures of animal consumption to estimate their efficiency (Arthur et al., 2004; Robinson and Oddy, 2004; Basarab et al., 2011).

Kleiber (1936) evaluated the energy metabolism and formulated an index that disregards individual measures of consumption of the animal for alternatively estimating the feeding efficiency. This approach could be a useful tool to select animals with high growth efficiency relative to body size. In fact, the Kleiber ratio (**KR**) is a measurement of growth efficiency, independently on body size (Kleiber, 1961). Inasmuch as KR is not dependable on specific information, this index becomes an economically viable alternative to estimate the feeding efficiency of herds. A high value

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for this index indicates a greater dilution of maintenance requirements. Animals having a high KR are considered efficient users of feed (Ghafouri-Kesbi et al., 2011).

However, to include KR in breeding programmes, it is necessary to have information on the genetic parameters of this trait (Grion et al., 2014), particularly to infer the relationship between KR and BW in a multitrait model at different ages. This is the first study to provide a comprehensible genetic interrelationship between the KR and BW in Limousin and Charolais herds. Therefore, the goal of this study was to estimate the genetic parameters for BWs and measures of KR in Charolais and Limousin beef cattle breeds at 210 and 365 days of age using Bayesian inference.

Material and methods

Database

The dataset used in the present study was provided by the Associazione Nazionale Allevatori delle razze bovine Charolaise e Limousine Italiane, encompassing BW of 73 018 Limousin and 30 566 Charolais individuals born between 1999 and 2018. The initial dataset included 133 079 records from 1 177 herds for Limousin and 35 747 records from 199 herds for Charolais. The BW values were recorded every 3 months between birth up to a maximum of 12 months. The number of BW values per individual ranged from 1 to 6.

Only individuals with, at least, two records and belonging to contemporary groups (i.e. animals born in the same herd, year and month) with a minimum of five records were retained. Finally, 14 508 Limousin (corresponds to 19% of the total number of individuals in the initial dataset) from a pedigree containing 30 409 individuals (882 sires and 7 913 dams) and 1 818 Charolais (corresponding to 6% of the total number of individuals in the initial dataset) from a pedigree containing 4 964 individuals (207 sires and 1 319 dams) were used in the analysis.

Body weight adjustment

Body weight values were adjusted at 60 (BW60), 210 (BW210) and 365 (BW365) days of age according to the following equations (Lôbo, 1992): $ABW_i = BW_b + ADG * d_{i-b}$ and, $ABW_i = BW_a - ADG * d_{a-i}$; where **ABW** was the adjusted weight at time *i* (*i* = 60, 210 and 365 days); **BW** was the recorded weight before (*b*) or after (*a*) time *i*; **ADG** was the average daily gain estimated between time *a* and time *b*; and *d* was the distance between time *i* and time *b* or between time *a* and time *i*. An example of ABW calculation is available in [supplementary material S1](#).

Kleiber ratio calculation

The KR at 210 (KR210) and 365 (KR365) days of age was estimated according to the following formula (Kleiber, 1936): $KR_i = \frac{ADG_j}{BW_k^{0.75}}$; where KR_i was the KR calculated at standard age *i* (210 or 365 days); ADG_j was the average daily gain *j* observed between final (210 or 365 days) and initial weight (210 or 60 days); BW_k was the initial weight at standard age *i* (210 or 365 days). An example of KR calculation is shown in [supplementary material S1](#).

Data analysis

The SAS software package, version 9.4 (SAS Inst. Inc., Cary, NC), was used to edit and estimate the different models for the genetic parameter estimates. The fixed effects of sex, contemporary groups, linear and quadratic age of the dam were considered in

the model since they proved to be significant ($P < 0.0001$). The estimation of variance components was performed based on a multi-trait animal model using the software GIBBS3F90 (Misztal et al., 2002). The general fitted model was $y = Xb + Za + Mm + Wp + e$, where: **y** = vector of the dependent variable (BW 210, BW 365, KR 210, and KR 365), **X** = fixed effects incidence matrix; **b** = vector of fixed effects, **Z₁** = incidence matrix of additive genetic effects; **a** = vector of random direct additive genetic effects, **M₂** = incidence matrix of maternal additive genetic effects; **m** = vector of maternal genetic effects; **W₃** = incidence matrix of permanent environmental effects; **p** = vector of permanent environmental effects, and **e** = vector of residuals. Matrix **X** is an incidence matrix relating phenotypic records in vector **y** to fixed effects in vector **b**, while **Z₁**, **M₂** and **W₃** are the incidence matrices relating phenotypic records to the additive, maternal and permanent effects, respectively. Therefore, based on the four traits used in combined analysis, the multiple-trait animal model is represented as follows:

$$\begin{bmatrix} y1 \\ y2 \\ y3 \\ y4 \end{bmatrix} = \begin{bmatrix} X1 & 0 & 0 & 0 \\ 0 & X2 & 0 & 0 \\ 0 & 0 & X3 & 0 \\ 0 & 0 & 0 & X4 \end{bmatrix} \begin{bmatrix} \beta1 \\ \beta2 \\ \beta3 \\ \beta4 \end{bmatrix} + \begin{bmatrix} Z1 & 0 & 0 & 0 \\ 0 & Z2 & 0 & 0 \\ 0 & 0 & Z3 & 0 \\ 0 & 0 & 0 & Z4 \end{bmatrix} \begin{bmatrix} m1 \\ m2 \\ m3 \\ m4 \end{bmatrix} + \begin{bmatrix} W1 & 0 & 0 & 0 \\ 0 & W2 & 0 & 0 \\ 0 & 0 & W3 & 0 \\ 0 & 0 & 0 & W4 \end{bmatrix} \begin{bmatrix} p1 \\ p2 \\ p3 \\ p4 \end{bmatrix} + \begin{bmatrix} e1 \\ e2 \\ e3 \\ e4 \end{bmatrix}$$

where the subscripts 1, 2, 3 and 4 represent BW210, BW365, KR210 and KR365, respectively. For this model,

$$E \begin{bmatrix} y1 \\ y2 \\ y3 \\ y4 \end{bmatrix} = \begin{bmatrix} X1 & 0 & 0 & 0 \\ 0 & X2 & 0 & 0 \\ 0 & 0 & X3 & 0 \\ 0 & 0 & 0 & X4 \end{bmatrix} \begin{bmatrix} \beta1 \\ \beta2 \\ \beta3 \\ \beta4 \end{bmatrix}$$

and the variance-covariance matrix for genetic effects is $G = G_0 \otimes A$ where:

$$G_0 = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a12} & \sigma_{a13} & \sigma_{a14} & \sigma_{am1} & 0 & 0 & 0 \\ \sigma_{a12} & \sigma_{a2}^2 & \sigma_{a23} & \sigma_{a24} & 0 & \sigma_{am2} & 0 & 0 \\ \sigma_{a13} & \sigma_{a23} & \sigma_{a3}^2 & \sigma_{a34} & 0 & 0 & \sigma_{am3} & 0 \\ \sigma_{a14} & \sigma_{a24} & \sigma_{a34} & \sigma_{a4}^2 & 0 & 0 & 0 & \sigma_{am4} \\ \sigma_{am1} & 0 & 0 & 0 & \sigma_{m1}^2 & \sigma_{m12} & \sigma_{m13} & \sigma_{m14} \\ 0 & \sigma_{am2} & 0 & 0 & \sigma_{m12} & \sigma_{m2}^2 & \sigma_{m23} & \sigma_{m24} \\ 0 & 0 & \sigma_{am3} & 0 & \sigma_{m13} & \sigma_{m23} & \sigma_{m3}^2 & \sigma_{m34} \\ 0 & 0 & 0 & \sigma_{am4} & \sigma_{m14} & \sigma_{m24} & \sigma_{m34} & \sigma_{m4}^2 \end{bmatrix}$$

The variance-covariance matrix for permanent environmental effects is as follows: $P = P_0 \otimes I_c$ Where:

$$P_0 = \begin{bmatrix} \sigma_{p1}^2 & \sigma_{p12} & \sigma_{p13} & \sigma_{p14} \\ \sigma_{p12} & \sigma_{p2}^2 & \sigma_{p23} & \sigma_{p24} \\ \sigma_{p13} & \sigma_{p23} & \sigma_{p3}^2 & \sigma_{p34} \\ \sigma_{p14} & \sigma_{p24} & \sigma_{p34} & \sigma_{p4}^2 \end{bmatrix}$$

The variance-covariance matrix for residual effects, **R**, is a block diagonal with each block representing one of the seven residual covariance matrices corresponding to a set of one, two, or three traits measured from each animal (Eler et al., 1995). An initial iteration number was obtained arbitrarily; using a single chain with

400 000 iterations, burn-in of 40 000 samples, with a saving interval every 10 cycles (thin). The convergence diagnosis was carried out using the method by Raftery and Lewis (1992), using an algorithm implemented in software R, through the Bayesian Output Analysis (BOA) package (Smith, 2005). The analysis proposed by Raftery and Lewis (1992) includes the convergence for a stationary distribution and finds the required chain size to estimate accurately the quantiles of parameter functions (Barbosa et al., 2008). The descriptive statistics of the posteriori distribution for each parameter was obtained from effective samples. Direct heritability for all variables was estimated using: $h^2 = \sigma_d^2 / (\sigma_d^2 + \sigma_m^2 + \sigma_{mpe}^2 + \sigma_e^2)$. Maternal heritability for all variables was estimated based on: $h_m^2 = \sigma_m^2 / (\sigma_d^2 + \sigma_m^2 + \sigma_{mpe}^2 + \sigma_e^2)$. The genetic correlation was extracted from the output in the software GIBBS3f90. The genetic correlation values between traits were calculated by the following formula: $r_i = \frac{\sigma_{aii\bar{a}}}{\sqrt{\sigma_{ai}^2 \sigma_{air}^2}}$ and an approximate estimate of the SE of correlation was obtained by the range in the highest density interval containing 95% of observations (Gonzales-Recio and Alenda, 2005).

Results

Genetic variability for Kleiber ratio and BWs at 210 and 365 days of age

The descriptive statistics for BW and KR values for both breeds was shown in Table 1 and was observed that the KR decreased 30% in the Limousin and 28% in the Charolais, as the individual gets older (between 210 and 365 days old). The average daily gain remained close between both analysed ages. In general, both breeds presented similar values for all traits. The estimates of genetic parameters for BW and KR are shown in Tables 2 and 3, respectively. The heritability of BW was high in Charolais (0.39 and 0.42 for BW210 and BW365, respectively) and moderate in Limousin (0.22 for both periods). On the other hand, the estimated heritability of KR was similar between both breeds at 365 days of age (0.44) whereas it proved to be higher in Charolais (0.40) than in Limousin breed (0.21) at 210 days of age.

Genetic correlations for Kleiber ratio and BWs at 210 and 365 days of age

In both breeds, the maternal effects, as shown by the magnitude of the estimated heritability values, influenced the BW as well as KR, especially in Charolais breed. The correlations between the two measures of BW were moderate in both breeds whereas genetic correlations between BW and KR ranged from low to moderate (Tables 4 and 5). A negative genetic correlation was also

observed between BW210 and K365 in both breeds. The largest genetic correlations showed the lowest probability intervals.

Discussion

Genetic variability for Kleiber ratio and BWs at 210 and 365 days of age

In general, the estimated values of heritability indicate possible genetic gains for all traits evaluated in both breeds. Nonetheless, Charolais breed exhibited higher genetic variation than Limousin, thus being favourable to greater gains. The KR decreased as the individual gets older, and this is probably related to the high metabolic requirements for growth in young animals whereas adult animals require energy for their maintenance. Figueiredo et al. (2019) also observed that animals with larger body structure had lower values of KR. Previous reports about the heritability of KR in cattle showed values of 0.22 in zebu breeds (Grion et al., 2014) and 0.31 in bulls of different breeds (Crowley et al., 2010). Therefore, these heritability values indicate that KR might be selected, thereby allowing genetic gains by direct selection.

For the BW heritability values, Bennett and Gregory (1996) found heritability values varying from 0.26 to 0.40 and 0.16 to 0.34 in BW at 200 and 368 days of age for Limousin and Charolais, respectively. In relation to Limousin breed, the heritability observed in this study for BW is close to those reported (0.25) by Keeton et al. (1996) and (0.19) by Van Niekerk and Neser (2006) for weight at weaning. El-Saied et al. (2006) and Phocas and Laloë (2004) found heritability of 0.29 and 0.13 respectively for the weaning weight in Charolais. These values are lower than those found in this study, and as far as we know, no studies comparing the heritability of KR in Limousin and Charolais cattle breeds are available so far.

Cattle, especially females, of large adult size are not desirable in breeding programmes, because the maintenance of these animals generates high feeding costs, since they need more nutrients to maintain their high weight (Malhado et al., 2009). This relationship between body size and feed intake reinforces the importance of the genetic evaluation joint to BW and KR. In addition, heifers that are not precocious for growth may take longer to reach reproductive age. This will impact in beef cattle production systems, because the reproductive efficiency is one of the most important components for improving efficiency and genetic gains (reduced intervals between generations) (Terakado et al., 2015).

In both breeds herein analysed, the maternal effect had a high influence on BW210 and BW365 heritability, while the maternal effect tends to decrease from 210 to 365 days of age in relation to KR values. Thus, maternal effects, have an effect up to the age of 1 year mainly for BW210 and BW365, since the contribution of

Table 1

Descriptive statistics for BW, Kleiber ratio, metabolic live weight, and average daily gain at 210 and 365 days of age in Limousin and Charolais animals.

| Trait | Limousin | | | | Charolais | | | |
|--------|----------|-------|---------|---------|-----------|-------|---------|---------|
| | Mean | SD | Minimum | Maximum | Mean | SD | Minimum | Maximum |
| BW210 | 247.73 | 37.56 | 153.50 | 337.99 | 242.77 | 32.34 | 169.56 | 323.70 |
| BW365 | 411.98 | 61.31 | 255.81 | 562.79 | 408.61 | 56.97 | 279.39 | 537.00 |
| KR210 | 1.64 | 0.21 | 1.10 | 2.20 | 1.60 | 0.21 | 0.88 | 2.28 |
| KR365 | 1.14 | 0.16 | 0.70 | 1.50 | 1.15 | 0.18 | 0.51 | 1.69 |
| Mw210 | 62.46 | 7.12 | 43.60 | 78.81 | 61.40 | 6.15 | 46.99 | 76.32 |
| Mw365 | 91.91 | 10.22 | 63.96 | 115.54 | 90.72 | 9.52 | 68.34 | 111.55 |
| ADG210 | 1.030 | 0.215 | 0.481 | 1.729 | 0.990 | 0.200 | 0.430 | 1.710 |
| ADG365 | 1.060 | 0.230 | 0.451 | 1.723 | 1.050 | 0.250 | 0.390 | 1.880 |

Abbreviations: BW210 = BW at 210 days of age; BW365 = BW at 365 days of age; KR210 = Kleiber ratio at 210 days of age; KR365 = Kleiber ratio at 365 days of age; Mw210 = metabolic live weight at 210 days of age; Mw365 = metabolic live weight at 365 days of age; ADG210: average daily gain at 210 days of age; ADG365: average daily gain at 365 days of age.

Table 2
Estimates of genetic parameters for BW at 210 (BW210) and 365 (BW365) days of age in Limousin and Charolais animals.

| Item | BW210 | | | | | | BW365 | | | | | |
|-----------|--------------|--------------|------------------|--------------|---------|---------|--------------|--------------|------------------|--------------|---------|---------|
| | σ^2_a | σ^2_m | σ^2_{mpe} | σ^2_r | h^2_a | h^2_m | σ^2_a | σ^2_m | σ^2_{mpe} | σ^2_r | h^2_a | h^2_m |
| Charolais | | | | | | | | | | | | |
| M | 271.07 | 80.05 | 82.79 | 260.05 | 0.39 | 0.11 | 1045.03 | 493.92 | 111.22 | 805.39 | 0.42 | 0.20 |
| SD | 70.12 | 30.41 | 22.73 | 44.18 | 0.08 | 0.04 | 297.30 | 163.43 | 76.65 | 168.59 | 0.09 | 0.06 |
| Me | 260.25 | 75.66 | 83.86 | 263.20 | 0.38 | 0.11 | 1018.00 | 485.55 | 98.48 | 811.95 | 0.42 | 0.20 |
| Mo | 260.30 | 100.50 | 101.90 | 243.10 | - | - | 1035.00 | 491.90 | 115.10 | 1021.00 | - | - |
| I 95% | 169.40 | 37.95 | 46.12 | 182.80 | 0.26 | 0.02 | 584.60 | 250.10 | 18.76 | 517.70 | 0.28 | 0.09 |
| | 395.80 | 137.30 | 118.40 | 328.30 | 0.51 | 0.19 | 1578.00 | 774.20 | 251.90 | 1077.00 | 0.57 | 0.31 |
| Limousin | | | | | | | | | | | | |
| M | 213.94 | 83.44 | 61.25 | 610.85 | 0.22 | 0.08 | 424.90 | 151.30 | 47.45 | 1257.96 | 0.22 | 0.08 |
| SD | 35.21 | 27.77 | 27.82 | 28.08 | 0.03 | 0.02 | 81.88 | 49.32 | 24.87 | 55.15 | 0.04 | 0.02 |
| Me | 212.20 | 78.24 | 72.56 | 609.70 | 0.22 | 0.08 | 421.30 | 149.60 | 55.33 | 1259.00 | 0.22 | 0.08 |
| Mo | 217.90 | 107.10 | 74.21 | 594.60 | - | - | 435.90 | 145.40 | 20.57 | 1267.00 | - | - |
| I 95% | 139.20 | 25.37 | 5.71 | 548.50 | 0.15 | 0.02 | 279.40 | 64.85 | 2.67 | 1122.00 | 0.16 | 0.01 |
| | 274.90 | 168.20 | 97.45 | 662.90 | 0.27 | 0.17 | 574.30 | 242.20 | 100.50 | 1348.00 | 0.29 | 0.18 |

Abbreviations: M: mean; Me: median; Mo: mode; I: confidence interval. σ^2_a = component of the direct genetic additive variance; σ^2_m : component of the maternal genetic additive variance; σ^2_{mpe} = component of the permanent environmental variance; σ^2_r = residual variance; h^2_a = direct heritability; h^2_m = maternal heritability.

Table 3
Estimates of genetic parameters for Kleiber ratio at 210 (KR210) and 365 (KR365) days of age in Limousin and Charolais animals.

| Item | KR210 | | | | | | KR365 | | | | | |
|-----------|--------------|--------------|------------------|--------------|---------|---------|--------------|--------------|------------------|--------------|---------|---------|
| | σ^2_a | σ^2_m | σ^2_{mpe} | σ^2_r | h^2_a | h^2_m | σ^2_a | σ^2_m | σ^2_{mpe} | σ^2_r | h^2_a | h^2_m |
| Charolais | | | | | | | | | | | | |
| M | 1.51 | 0.76 | 0.10 | 1.33 | 0.40 | 0.20 | 1.30 | 0.51 | 0.20 | 0.85 | 0.44 | 0.17 |
| SD | 0.54 | 0.23 | 0.09 | 0.28 | 0.11 | 0.06 | 0.49 | 0.17 | 0.09 | 0.27 | 0.12 | 0.05 |
| Me | 1.49 | 0.73 | 0.07 | 1.35 | 0.41 | 0.20 | 1.21 | 0.49 | 0.20 | 0.89 | 0.43 | 0.16 |
| Mo | 1.29 | 1.03 | 0.11 | 1.24 | - | - | 1.31 | 0.47 | 0.25 | 1.00 | 0.41 | - |
| I 95% | 0.65 | 0.42 | 0.01 | 0.83 | 0.21 | 0.11 | 0.61 | 0.25 | 0.05 | 0.32 | 0.25 | 0.09 |
| | 2.44 | 1.18 | 0.29 | 1.74 | 0.56 | 0.32 | 2.25 | 0.82 | 0.36 | 1.25 | 0.65 | 0.28 |
| Limousin | | | | | | | | | | | | |
| M | 9.83 | 3.45 | 1.20 | 33.06 | 0.21 | 0.07 | 3.28 | 1.04 | 0.08 | 3.36 | 0.41 | 0.13 |
| SD | 1.39 | 0.60 | 0.41 | 1.01 | 0.02 | 0.01 | 1.39 | 0.49 | 0.02 | 0.77 | 0.08 | 0.05 |
| Me | 9.78 | 3.40 | 1.24 | 33.08 | 0.21 | 0.07 | 2.95 | 0.97 | 0.08 | 3.53 | 0.39 | 0.14 |
| Mo | 10.02 | 3.33 | 1.24 | 32.91 | - | - | 2.73 | 1.01 | 0.10 | 3.47 | 0.39 | - |
| I 95% | 6.85 | 2.27 | 0.39 | 30.64 | 0.15 | 0.01 | 2.28 | 0.54 | 0.02 | 0.10 | 0.33 | 0.01 |
| | 12.21 | 4.55 | 1.86 | 34.70 | 0.25 | 0.15 | 7.71 | 2.32 | 0.15 | 3.83 | 0.70 | 0.26 |

Abbreviations: M: mean; Me: median; Mo: mode; I: confidence interval. σ^2_a = component of the direct genetic additive variance; σ^2_m : component of the maternal genetic additive variance; σ^2_{mpe} = component of the permanent environmental variance; σ^2_r = residual variance; h^2_a = direct heritability; h^2_m = maternal heritability.

Table 4
Genetic correlation for BWs and Kleiber ratio in Limousin animals.

| Item | BW210 | BW365 | KR210 | KR365 |
|-------|----------------------|--------------------|----------------------|-------|
| BW210 | - | | | |
| BW365 | 0.76 (0.64 0.84) | - | | |
| KR210 | 0.52 (0.47 0.61) | 0.29 (0.14 0.37) | - | |
| KR365 | -0.27 (-0.34 0.06) | 0.40 (0.28 0.53) | -0.15 (-0.21 0.02) | - |

Abbreviations: BW210 = BW at 210 days of age; BW365 = BW at 365 days of age; KR210 = Kleiber ratio at 210 days of age; KR365 = Kleiber ratio at 365 days of age. Highest density interval containing 95% of the observations for genetic correlations is shown in parentheses.

Table 5
Genetic correlation for BWs and Kleiber ratio in Charolais animals.

| Item | BW210 | BW365 | KR210 | KR365 |
|-------|-----------------------|--------------------|---------------------|-------|
| BW210 | - | | | |
| BW365 | 0.66 (0.58 0.78) | - | | |
| KR210 | 0.65 (0.54 0.71) | 0.21 (0.14 0.30) | - | |
| KR365 | -0.35 (-0.45 -0.28) | 0.56 (0.48 0.62) | 0.11 (-0.03 0.18) | - |

Abbreviations: BW210 = BW at 210 days of age; BW365 = BW at 365 days of age; KR210 = Kleiber ratio at 210 days of age; KR365 = Kleiber ratio at 365 days of age. Highest density interval containing 95% of the observations for genetic correlations is shown in parentheses.

the dam to the phenotype of her offspring occurs through the transmission of genetic effects and through the expression of maternal effects. As a practical result, selecting dams with lower maternal ability and ability to produce milk may have an effect on offspring BWs, which is an important economic trait in the beef industry. Therefore, the maternal effect should be included in the genetic estimates for BW up to 1-year-old animals and the non-inclusion in the genetic model may interfere with the evaluation result (genetic values). However, further studies are needed to better contextualise the maternal effects on adult beef cattle BWs.

Genetic correlations for Kleiber ratio and BWs at 210 and 365 days of age

The genetic correlations between the two ages herein analysed for BW were moderate (Charolais = 0.66; Limousin = 0.76). Favourable and high genetic correlations between BW values have been reported in previous studies with other breeds (Bolognon et al., 2009; Meyer et al., 2004). These results indicate a positive impact on selection since they allow the use of BW records of young animals, thus leading to reduction of generation intervals in genetic improvement programmes. Furthermore, the genetic correlations between the two ages herein analysed for KR were low (Charolais = 0.11; Limousin = -0.15). This difference suggests that these traits should be analysed separately in each period of their life stage.

The genetic correlations between BW210 and KR365 were low and negative in both breeds indicating that some animals with high BW210 may show less growth efficiency (KR365) at older ages. In general, animals with higher KR values demanded less maintenance requirements from weaning period on, i.e. they are able to reach high body growth without increasing maintenance costs. However, taking into account the moderate correlation between KR365 and BW365 in both breeds, it is possible that selecting for either trait means similar alleles might be under selection, but more importantly, it reveals that animals with high KR values can be selected without great influence on BW. This result is positive and at the same time, it presents disagreements with the conventional method used to calculate the feeding efficiency. As a matter of fact, the estimates of conventional feeding efficiency are obtained from the ratio between feed consumption and weight gain, and feed conversion is calculated by the inverse of this relationship (Schenkel et al., 2004).

Thus, its use as a criterion for the identification of efficient animals is limited, since they are gross measures that disregard putative differences in the maintenance and growth requirements of animals (Berry and Crowley, 2012). Consequently, increases in adult size are usually followed by increased nutritional requirements. It should also be considered that the use of these relationships in selection programmes may result in issues related to the prediction of changes in the traits of further generations, since animals may present similar efficiency with different feed consumption and weight gains (Hoque and Suzuki, 2009).

This statement is supported by the report by Arthur et al. (2001), who verified that the feed conversion rate was highly and negatively genetically correlated with relative growth rate ($r = -0.90$) and KR ($r = -0.81$). The relative growth rate is also independent of food intake estimates. Similarly, negative genetic correlations between feed efficiency and BW in cattle were reported by Crowley et al. (2010), and Berry and Crowley (2012). According to these authors, feeding efficiency presents favourable genetic correlation with traits related to feed consumption and weight gains, indicating correlated responses when these traits were selected. Castilhos et al. (2010) also found that KR was the trait with the strongest correlation with average daily gain, when they compared

the correlation coefficient values between weight and indices of food conversion, residual gain, and relative growth rate.

Environmental factors should also be considered, as global livestock farming is adjusting their strategies due to the pressure by international communities in relation to the role of cattle production in climate change. Animals with good feeding efficiency lead to decreased gas emission per unit of weight produced, mainly because of the reduction in daily food consumption (Herd et al., 2002). Therefore, further approaches focusing on the genetic correlation between KR and gas emission in beef cattle are encouraged to optimise the production of Charolais and Limousin beef cattle breeds.

Conclusions

The genetic variability of KR is likely to allow satisfactory genetic gains. In addition, this index is not dependent on measurements of food consumption, thus favouring the evaluation of large herds, where individual consumption is extremely difficult to be measured. The genetic correlations between both estimated values ranged from low to moderate, indicating that a correlated response could not be inferred. In fact, selection over KR has no effects on BW, besides reducing the costs for evaluation of herds. The heritability estimates indicated possible genetic gains for BWs in both breeds. However, since we observed a moderate genetic correlation of BWs between ages, information based only on young animals for selection is not recommended to predict the BW at older ages.

Supplementary materials

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.animal.2022.100528>.

Ethics approval

Not applicable. Approval by the committee of animal welfare and use was not necessary because the database used in this study was obtained from pre-existing databases based on routine animal recording procedures.

Data and model availability statement

None of the data were deposited in an official repository. The data used in this study are in the Associazione Nazionale Allevatori Delle Razze Bovine Charolaise e Limousine (<https://www.anacli.it>) database. These data were collected from commercial beef farms, and thus, the information is accessible only with permission from the herd owners. Data may be available upon request by contacting the corresponding author.

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Declaration of interest

The authors declare no conflicts of interest.

Acknowledgement

Associazione Nazionale Allevatori Delle Razze Bovine Charolaise e Limousine.

Financial support statement

This research was funded by Associazione Nazionale Allevatori Delle Razze Bovine Charolaise e Limousine, grant number 2015.99.2264.1127.

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