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Alternative measures of cow–calf efficiency for Afrikaner, Bonsmara, Nguni, Angus and Simmental sired calves

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ABSTRACT

Context. It is desirable to identify cows that produce higher weaning weights while consuming less feed in order to increase biological efficiency; however, there is no universally accepted metric for cow–calf efficiency. **Aim.** Due to the common usage of ratios to express biological cow efficiency, despite their theoretical defects, these measures and alternatives to them were examined to understand better some of the complexities in improving cow efficiency. **Methods.** The analyses were carried out using SAS. In model 1, 205-day calf weight/cow weight was used to define cow–calf efficiency and in model 3, 205-day calf weight per Large Stock Unit (LSU), which is a standard unit of energy consumed, was used to quantify efficiency. In models 2 and 4, 205-day calf weight was analysed using cow weight and Large Stock Unit, respectively, as covariates. **Key results.** The use of ratios was biased in favour of the smaller Nguni cows. The Bonsmara and Angus sired calves attained 53% of the weight of their Nguni dams, and their weaning weight per Large Stock Unit was 169 ± 9 kg. However, Angus sired calves from Bonsmara dams were most efficient when efficiency was determined by analysis of covariance when cow weight and Large Stock Unit were used as covariates (162 ± 17 kg and 133 ± 22 kg), respectively. **Conclusions.** The results indicate the difficulty in determining differences in cow–calf efficiency in the absence of a standard definition. The difference between output and input can be maximised, when traits are reported in consistent units like joules, financial currency, or carbon footprint. **Implications.** This inconsistent definition of cow–calf efficiency makes its improvement challenging.

Keywords: analysis of covariance, breed additive effects, cow weight, crossbreeding, efficiency, large stock unit, ratios, weaning weight.

Introduction

While increasing the weight of calf weaned or reducing cow intake, *ceteris paribus*, will increase efficiency it might be more desirable to identify cows that produce higher weaning weights while consuming less feed, as this is a form of high output and low input productivity that Davis *et al.* (1983*a*, 1983*b*) described. Efficiency is a multifactorial and complex trait in beef cattle and variation among animals in it stems from the interaction of many biological processes (Kenny *et al.* 2018). Annual efficiency may be defined as the relationship between the weight of the calf that is produced and the input of feed that is necessary to sustain the cow and allow her to nourish her calf (MacNeil *et al.* 2017*a*; Sessim *et al.* 2020). Despite favouring smaller cows, the ratio of calf weight at weaning to cow weight (CWT) has frequently been used as a proxy for biological efficiency (e.g. Dickerson and Grimes 1947; Frahm and Marshall 1985; Lemes *et al.* 2017). The use of the ratio of calf weight at weaning to cow weight as a measure of a cow's individual efficiency and to facilitate matching cow size to their production environment continues through the present time (e.g. Thompson *et al.* 2020; Farrell *et al.* 2021). However, there are statistical issues that result from the use of ratios. Variables expressed as ratios are skewed to the right and leptokurtic with non-normality increasing as the magnitude of the denominator's coefficient of variation increases

(Atchley *et al.* 1976). Curran-Everett (2013) explicitly states, 'There is peril lurking in a ratio: only if the relationship between numerator and denominator is a straight line through the origin will the ratio be meaningful. If not, the ratio will misrepresent the true relationship between numerator and denominator'. In contrast, regression techniques, including analysis of covariance, are versatile and they can accommodate an analysis of the relationship between numerator and denominator when a ratio is useless. Yet despite these issues, the definition of biological efficiency is not entirely consistent in the literature (MacNeil *et al.* 2017*b*).

In South Africa, Meissner *et al.* (1983) developed the concept of a 'Large Stock Unit' (LSU) in an attempt to classify grazing animals in a way that would reflect differences among them based on the metabolisable energy requirements for specific age groups, weights, and phases of production (growing, mature, dry, pregnant and lactating) of cows. The originally intended purpose for LSU was in the management of natural pastures in order to avoid unsustainable grazing pressure as overgrazing had resulted in degradation of this natural resource in South Africa. A LSU is defined as the equivalent of an ox requiring 75 MJ of metabolisable energy to maintain a live weight of 450 kg and gain 500 g per day on a grass pasture that has a mean digestible energy of 55%. Whereas differences in the ratio of weight to height can be used to indicate fatness and fatter cows have lower energy requirements than less fat cows (Klosterman *et al.* 1968; Thompson *et al.* 1983) separate predictions of LSU according to frame size are justified. Thus, LSU are predicted as quadratic functions of body weight with different functions being applied to cows that differ in frame size (Mokolobate *et al.* 2015). However, at present the energy requirement of a calf accompanying its dam and her milk production are not taken into consideration in the estimation of LSU. The ratio of weaning weight to LSU is viewed as being conceptually similar to an efficiency metric that is expressed relative to the area of land that is required to sustain a cow with constant grazing intensity (LSU/ha).

The common usage of ratios to express cow efficiency, despite their theoretical defects, provided motivation to examine ratio measures of efficiency and alternatives to them in order to understand better some of the complexities in improving cow efficiency. The explicit objective of this study was to use differences among breed groups in measures of cow–calf production efficiency to illustrate ways in which the mathematical definition of efficiency can affect it in evaluating differences among the breed groups. The data used herein originated from a crossbreeding study that employed Bonsmara (medium frame size), Afrikaner and Nguni (small frame size) cows (Pyoos *et al.* 2020).

Materials and methods

Study site

The study was ethically cleared by the Agricultural Research Council – Animal Production Institute Ethical Committee, with reference APIEC 18/16. The data was recorded between 2014 and 2016 at the Vaalharts research station, situated near Jan Kempdorp in the Northern Cape province of South Africa. The research station is located in the centre of South Africa at 27°51′ South and 24°50′ East at an altitude of 1175 m and is in an area with sandy red soil with lime rock underneath. These soils form part of the Hutton formation and represent mainly the Manganese series (Laker 2003). The veld type is mixed *Tarchonanthus* veld, Veld type No 16b, 4 (Acocks 1975). The research station has a recommended carrying capacity of 10 ha/LSU. The climate at the Vaalharts research station is characterised by hot summers and cold winters with frost a common occurrence. The highest monthly average temperature is around 32°C and is experienced during December and January and the lowest monthly average temperature is around −0.5°C and is experienced during July. The average precipitation is around 450 mm per annum of which 88% is experienced during the summer months from October to April in the form of thunderstorms.

Data collection

The data were collected according to the approved standard operating procedures of the National Beef Recording and Improvement Scheme in South Africa, which is accredited with the International Committee for Animal Recording (ICAR). The data resulted from mating Afrikaner (AF), Bonsmara (BN), Nguni (NG), Angus (AN) and Simmentaler (SM) bulls to AF, BN, and NG cows over a 3-year period. For details of the data collection and genetic modelling of the breed groups and prediction of performance of the crossbreeding systems, see Pyoos *et al.* (2020).

A total of 576 cows were used in this study. A BN herd has been kept at Vaalharts since 1986, with BN cows from the Wesselsvlei line being introduced there in 2008. An NG herd was established at Vaalharts between 2007 and 2008. The AF herd was acquired specifically for this research. The purchased AF and NG cows originated from herds in Central Free State (N = 59), Southern Free State (N = 3), Northern Cape (N = 21), North West (N = 11), Eastern Cape (N = 5), Limpopo (N = 30), Mpumalanga (N = 9), and Namibia (N = 8).

At the beginning of the study, the cows were stratified by their age, weight and profile of estimated breeding values, within each breed. They were then assigned to mating groups within strata to avoid the possibility of uneven genetic merit of cows mated to any breed of bull. With the exception that some of the AF cows were pregnant when they were purchased, each bull was used across the three breeds of dam and there was connectedness of sires across years. The mating season was in summer, from 1 December until 28 February. At least two bulls of each breed were assigned to a specific mating group. Thus, the AF, BN and NG cows produced calves sired by AF, BN, NG, AN and SM bulls. In year 1, single sire mating was used, whereas in years 2 and 3 multiple-sire mating was used and paternal parentage is therefore unknown. The fifteen breed groups and numbers of calves produced are shown in Table 1.

Breeding occurred on natural veld pastures that contained bulls from one breed of sire. After the breeding season, all cows were kept in one herd until calving. As the cows calved, they were moved to another paddock with the other cow–calf pairs. All calves were raised by their dams from birth through weaning at approximately 205 days old. Birth dates were recorded and calves were weighed within 48 h of birth. Each year, all calves were weaned and weighed on the same day.

Cows were culled voluntarily when they did not meet minimum breed standards for fertility. Thus, 48 cows were replaced with 2-year-old heifers of the same breed from animals that were produced in this project or were purchased through the breed society or at auctions that were held under the auspices of the society. Involuntarily culled cows (death, injury, old age, etc.) were replaced in a similar way. Management of the cattle was according to requirements set out in the manual of the Agricultural Research Council (ARC) for active participation in the National Beef Cattle Improvement Scheme. Strict cognisance was taken of contemporary group effects, especially the nutritional status of the different groups in the herd. Bulls received supplementary feeding prior to the breeding season, to ensure that they reached a body score condition of 3.5 out of five before the mating season began.

Statistical models

Four analyses, which imply alternative definitions of cow–calf efficiency, were carried out using PROC MIXED of the SAS™ System for Windows (ver. 8.2; SAS Institute Inc., Cary, NC, USA). All the analyses included several common features. The linear models included fixed categorical effects for year (2014, 2015 or 2016) and sex of calf (male or female), fixed linear and quadratic effects were included for age of the cow, and fixed linear effects were included for the individual breed additive effects of Afrikaner (g^{i}_{AF}), Nguni (g^{i}_{NG}), Simmentaler (g^{i}_{SM}), and Angus (g^{i}_{AN}), for maternal breed additive effects of Afrikaner (g^{m}_{AF}) and Nguni (g^{m}_{NG}), and for breed-specific individual heterosis effects as manifest in Afrikaner–Nguni (h^{i}_{AN}), Bonsmara–Nguni (h^{i}_{BN}) and Afrikaner–Bonsmara (h^{i}_{AB}) crosses. The simultaneous equations were made full rank by deletion of the individual and maternal breed additive effects of Bonsmara.

In addition, breed-specific heterosis effects from crosses that involved Simmentaler and Angus were not estimable and these heterosis effects were assumed equal to the average of the estimable heterosis effects from the 3 × 3 diallel of Afrikaner, Bonsmara and Nguni. Finally, all the models included random effects for herd-of-origin nested within breed to account for any random variation attributable to the source of the cows and to account for the permanent environmental effect arising from cows that produced more than one calf. The dependent variable for the first analysis was the ratio of 205-day calf weight to cow weight (EFF1). The second analysis was an analysis of covariance that included the linear effect of cow weight on 205-day calf weight (EFF2). The third (EFF3) and fourth (EFF4) analyses were similar to the first and second analyses, respectively, with cow weight replaced by LSU.

The cow weights at weaning and their respective LSUs were used to develop an equation to calculate the LSU for different weights for lactating beef cows (Neser *et al.* 2012). Thus, in models 1 and 3, the implicit assumption is that the relationship between 205-day weight and cow size is linear and that line passes through the origin. In models 2 and 4, the second part of that assumption is negated and the relationship between 205-day calf weight and cow weight was determined by the data.

Results

As a point of reference, means for 205-day weight from each of the 15 breed groups originally presented in Pyoos *et al.* (2020) are presented in Table 2. Weights adjusted to 7-year of age for Afrikaner, Bonsmara and Nguni cows (Pyoos *et al.* 2020) were on average 446 ± 10 kg, 454 ± 10 kg and 365 ± 7 kg (mean ± s.e.), respectively. The corresponding LSUs were 1.31, 1.41 and 1.14, respectively.

Table 1. The crossbreeding plan indicating the total number of calves that were weaned in each of the mating groups between 2014 and 2016.

Breed of dam	Breed of sire				
	Afrikaner	Bonsmara	Nguni	Angus	Simmentaler
Afrikaner	33	12	12	9	6
Bonsmara	21	78	39	33	30
Nguni	54	54	117	39	42

Table 2. 205-day weaning weights (mean ± s.e.) of calves produced in 2014–2016 study of cow efficiency.

Breed of sire	Breed of dam		
	Afrikaner	Bonsmara	Ngumi
Afrikaner	192 ± 9	216 ± 13	187 ± 7
Angus	204 ± 9	224 ± 13	195 ± 7
Bonsmara	202 ± 10	218 ± 13	193 ± 7
Nguni	198 ± 10	218 ± 13	185 ± 6
Simmentaler	198 ± 9	218 ± 13	189 ± 7

Breed-specific genetic effects for the four measures of cow–calf efficiency are presented in Table 3. In the environment of the Vaalharts research station during 2014–2016, the individual breed additive effects were less for AF and possibly NG than BN irrespective of the measure that was used. Both AN and SM breed additive effects were more similar to BN. Differences among maternal breed additive effects appeared negligible. Individual heterosis for efficiency was less than 1% of the straightbred mean, irrespective of how it was calculated. However, the individual heterosis effects were more likely to be significant when cow–calf efficiency was expressed as a ratio as compared to its determination from analysis of covariance. This inconsistency among the measures of cow–calf efficiency makes clarity regarding differences among genetic effects on true efficiency illusive.

Use of ratios presented in Table 4 to quantify cow–calf efficiency favoured calves from the smaller Nguni dams. With the ratio measures of efficiency (EFF1 and EFF3), the NG breed of dam was 9.4% superior to BN and 11.8% superior to AF when the denominator was cow weight and these differences diminished to approximately 6.0% and 5.9%, respectively, when the denominator was LSU. The same comparisons were quite different when efficiency was evaluated with analysis of covariance (EFF2 and EFF4). The NG was 6.6% and 5.5% less efficient than BN using cow weight and LSU, respectively, as the covariate. In comparison to the AF, on the same bases, the NG was 0.3% and 0.7% more efficient. The advantage of Nguni dams in EFF1 and EFF3 results from the implicit assumption of zero intercepts by the ratio measures as opposed to the positive intercepts of the best fit regression equations that describe the relationship of weaning weight and cow weight. Thus, it can be concluded that the ratio measures of the relationship between weaning weight and cow size introduce bias into the comparisons that is not supported by the *ad hoc* consideration of the data.

Discussion

Benefits from crossbreeding are common knowledge (e.g. Williams *et al.* 2010; Theunissen *et al.* 2013). Dadi *et al.* (2002) proposed that crossbreeding might facilitate improvement of production under various climatic conditions. Leal *et al.* (2018) found crossbreeding to be beneficial to increase beef cattle performance from birth to slaughter in the challenging environment of southern

Table 3. Breed specific direct and maternal additive effects expressed as deviations from the Bonsmara effects (i.e. $g^i_{BN} = g^m_{BN} = 0$) and individual heterosis effects on four measures of efficiency expressed as traits of the calf.

Genetic effects	Measures of cow–calf efficiency			
	EFF1 (%)	EFF2 (kg)	EFF3 (kg/LSU)	EFF4 (kg)
g^i_{AF}	−9.2 ± 3.1*	−20.7 ± 11.2†	−23.3 ± 9.1	−20.8 ± 11.2†
g^i_{NG}	−3.6 ± 2.2†	−10.8 ± 7.8	−9.8 ± 6.4*	−11.0 ± 7.8
g^i_{AN}	−1.5 ± 3.0	1.6 ± 10.8	−2.4 ± 8.9	1.6 ± 10.8
g^i_{SM}	−5.6 ± 3.0†	−13.4 ± 10.8	−15.1 ± 8.9†	−13.5 ± 10.8
h^i_{AB}	1.9 ± 1.9	2.6 ± 6.7	5.1 ± 5.6	2.5 ± 6.7
h^i_{AN}	4.6 ± 1.7*	9.8 ± 6.0	11.8 ± 4.9*	9.8 ± 6.0
h^i_{BN}	2.0 ± 1.2†	4.2 ± 4.3	5.3 ± 3.6	4.1 ± 4.3
h^i	2.8 ± 1.1*	5.5 ± 4.0	7.4 ± 3.3*	5.5 ± 4.0
g^m_{AF}	2.9 ± 3.4	−6.5 ± 15.1	11.9 ± 11.0	−1.8 ± 15.1
g^m_{NG}	5.4 ± 2.7*	−11.0 ± 12.6	14.0 ± 8.8	−6.2 ± 12.9

EFF1 = 100 × 205-day weight/cow weight; EFF2 = 205-day weight analysed with cow weight as a linear covariate; EFF3 = 205-day weight/LSU; where LSU = the equivalent of an ox requiring 75 MJ of metabolisable energy to maintain a live weight of 450 kg and gain 500 g per day on a grass pasture that has a mean digestible energy of 55%; and EFF4 = 205-day weight analysed with LSU as a linear covariate.

g^m_k = direct additive effect of breed k; h^i = the individual heterosis effect attributable to the combination of breeds indicated by the subscript, and g^i_k = maternal additive effect of breed k.

†$P < 0.10$; *$P < 0.05$.

AF, Afrikaner; BN, Bonsmara; NG, Nguni; AN, Angus; SM, Simmentaler.

Table 4. Estimates of four alternative measures of cow efficiency (mean ± s.e.) for Afrikaner, Bonsmara, Nguni, Angus and Simmentaler sired calves from Afrikaner, Bonsmara and Nguni dams of a constant age.

Dam breed	EFF	Sire breed				
		AF	BN	NG	AN	SM
AF	1 (%)	41 ± 2	48 ± 2	47 ± 2	47 ± 2	45 ± 2
	2 (kg)	129 ± 15	144 ± 15	139 ± 15	145 ± 15	138 ± 15
	3 (kg/LSU)	141 ± 6	160 ± 7	155 ± 7	159 ± 6	153 ± 6
	4 (kg)	104 ± 20	120 ± 19	115 ± 19	121 ± 19	113 ± 19
BN	1 (%)	45 ± 3	47 ± 2	47 ± 2	47 ± 2	47 ± 2
	2 (kg)	151 ± 17	156 ± 17	139 ± 15	145 ± 15	155 ± 17
	3 (kg/LSU)	148 ± 8	153 ± 8	155 ± 7	159 ± 6	152 ± 8
	4 (kg)	122 ± 22	127 ± 22	115 ± 19	121 ± 19	126 ± 22
NG	1 (%)	53 ± 2	49 ± 2	49 ± 1	53 ± 2	51 ± 2
	2 (kg)	145 ± 12	134 ± 12	134 ± 12	146 ± 12	138 ± 12
	3 (kg/LSU)	169 ± 5	157 ± 5	158 ± 5	168 ± 5	161 ± 5
	4 (kg)	121 ± 16	110 ± 17	110 ± 16	122 ± 16	114 ± 16

Bonsmara and Nguni dams of a constant age.
EFF1: 100 × 205-day weight/cow weight, EFF2: 205-day weight analysed with cow weight as a linear covariate, EFF3: 205-day weight/LSU. Where LSU = the equivalent of an ox requiring 75 MJ of metabolisable energy to maintain a live weight of 450 kg and gain 500 g per day on a grass pasture that has a mean digestible energy of 55%, and EFF4: 205-day weight analysed with LSU as a linear covariate.
AF, Afrikaner; BN, Bonsmara; NG, Nguni; AN, Angus; SM, Simmentaler.

Brazil, where a level of tropical adaptation is needed. Cundiff *et al.* (1986) found heterosis effects were important in determining production efficiency, but not nearly as large as the range for additive genetic differences between breeds in a temperate environment. Breed additive effects and heterosis may significantly impact traits influencing reproduction, calf survival, milk production, growth rate, and longevity in beef cattle (Gregory and Cundiff 1980). Thus, a first step in predicting the outcome from a crossbreeding system is to understand the direct and maternal breed additive and heterosis effects for the specific breeds that are available (Dickerson 1969; Dillard *et al.* 1980; Robison *et al.* 1981). It is deemed desirable that crossbreeding systems be designed in a way that maximises efficiency.

In this study the Nguni cows had higher values than Afrikaner and Bonsmara cows when biological efficiency was expressed as a ratio either to body weight or LSU, as expected. This result arises not due to a biological difference between the breeds in efficiency, but rather due to the bias that results from the implicit assumption that ratios describe a linear relationship that passes through the origin (Curran-Everett 2013). This assumption belies the fact that cows have maintenance requirements that are related to their body weight (e.g. NRC 2016).

Cundiff *et al.* (1986) observed that variation among breeds in efficiency was much greater for additive effects than for heterosis, without intending to imply that the effects of heterosis were not important. Differences among breeds are also highly heritable and thus amenable to rapid utilisation. However, in the present study even the differences in breed additive effects were not large. Heterosis for efficiency was less than 1% of the straightbred mean, whereas individual heterosis for 205-day calf weight was 1.5% in these data (Pyoos *et al.* 2020). Maternal heterosis for 205-day weight and cow weight were not estimable in these data due to the absence of crossbred cows. Cartwright (1970) suggested that complementarity among breeds be exploited by mating crossbred cows of small to medium size that produce an optimal amount of milk to bulls of another breed characterised by rapid carcass growth. Without recognising the statistical defects of ratio measures, Lemes *et al.* (2017) concluded that because of their lower nutritional requirements, cows of small and moderate biotypes and lower total milk production are more efficient than cows of larger biotypes and higher milk production in pasture-raised beef systems. In examining various crossbreeding systems, MacNeil *et al.* (1988) found weaning weight per cow exposed for breeding increased by 18–23% due to heterosis that is captured in rotational crossing systems relative to straightbred performance.

In the present study, differences in breed additive effects on the component traits (Pyoos *et al.* 2020) and on measures of efficiency were less than in the aforementioned studies. One partial explanation for these effects not being as readily detected as may have been anticipated a priori, is the increased residual variance of them relative to other crossbreeding studies (Pyoos *et al.* 2020). However, this study took place under the quasi-commercial conditions of the Vaalharts Research Station rather than in a more tightly controlled situation. A second explanation for failure to detect differences in breed additive effects may result from decreased expression of genetic potential in this environment as opposed to a more favourable one. This environmental modification of genetic expression, referred to as genetic de-canalisation/canalisation, was demonstrated to occur frequently in drosophila reared at different temperatures (Huang *et al.* 2020). In beef cattle, MacNeil *et al.* (2017*b*) also found the expression of both direct and maternal additive effects on gain from birth to weaning to be environmentally sensitive. Farrell *et al.* (2021) found that published data suggested heavier cows to be less efficient when measured as the ratio of calf weaning weight relative to cow live weight, and thus herds of lighter cows were predicted to be more profitable. The wide diversity of environments in which beef cattle are farmed with worldwide, makes careful consideration of cow size important to maximise efficiency (Arango and Van Vleck 2002).

It would be remiss not to mention the importance of reproduction in evaluating cow efficiency (Cundiff *et al.* 1992; Burns *et al.* 2010). Schoeman *et al.* (1993) examined an annualised efficiency as measured by the weight of calf weaned divided by the metabolic weight of its dam adjusted for differences in calving interval for AF, SM and Hereford and various crosses among them. A reanalysis of the results from that study using methods similar to those employed here indicated individual and maternal heterosis for annualised efficiency to be 7% and 6% of the purebred means, respectively. Scholtz *et al.* (2022) discuss incorporating inter-calving period in an index of biological efficiency that can be used in the evaluation of animals within a breed. However, while it would be desirable to include reproductive rate in any evaluation of cow efficiency the present data are not sufficient to provide such an evaluation. Further, length of productive life (Morales *et al.* 2017) could also have important effects on biological efficiency on a production system basis, but again such data were not available in this study due to the data having been collected only over a period of 3 years.

A full life-cycle econometric evaluation of production efficiency may be an obvious alternative to the annual evaluation of biological efficiency that forms the basis of this study. Such an evaluation depends on the ability to assign economic values to weaning weight as a source of revenue and the feed consumed by the cow producing a calf as a cost. For each breed group, the profit maximising weaning weight is at the level of production where the marginal revenue is equal to the marginal cost. However, the required economic values are not known without error, particularly since the operative values that apply to a management decision are those that will be realised going forwards. Thus, the focus of this study was on methods for evaluating biological efficiency. However, the findings of this study that are relative to the methods of calculating efficiency would still apply when input and output are measured in economic units.

The focus of the current investigation was solely on the commonly used combination of weaning weight and cow size to facilitate the comparison of breeds for biological efficiency. Future research will entail the reproductive performance and longevity of the breed groups from which the data used herein originated and to provide a more comprehensive evaluation of their production efficiency. It will also be important to better characterise the life-cycle feed consumption of the indigenous breeds of South Africa.

Conclusions

Regardless of how biological efficiency was expressed, production of crossbred calves increased it. However, the results illustrate the difficulty in determining differences in efficiency in the absence of a standard definition for this index. Inconsistencies in results arose depending on whether efficiency was defined by a ratio or through analysis of covariance. Due to unrealistic assumptions in their calculation, the use of ratios as measures of cow–calf weaning efficiency cannot be recommended. One potential alternative would be to maximise the difference between output and input when the traits are reported in consistent units such as joules, kg protein, local currency, or carbon.

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Data availability. This work was initiated by the first author as part of a MSc study. As the data will be used for further research, it is not currently available in raw form.

Conflicts of interest. The authors declare that they have no conflicts of interest with regard to this work.

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