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Body composition and composition of gain of growing beef bulls fed rations with varying energy concentrations

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ABSTRACT

Data on chemical body composition of cattle serve as a basis for recommendations on energy and nutrient requirements. Relevant data of growing dual-purpose Fleckvieh (German Simmental) bulls are scarce and originate from old trials, covering low rates of gain and live weights. Hence, the aim of the study was to analyze the body tissue distribution, chemical composition, and composition of body weight gain of growing Fleckvieh bulls within a 120–780 kg live weight range. Results showed that body composition changed during growth but was not affected by dietary energy concentration. Changes in body composition were characterized by increasing shares of fat tissue and ether extract. Body tissues as blood, organs, gastrointestinal tract, and bone proportionately decreased during growth, while muscle and tendon proportions remained constant. The bulls featured enhanced growth potential and high muscle and protein gain throughout the described weight range. The requirements for metabolizable protein in relation to energy decrease with increasing live weight of the animals.

1. Introduction

Body composition of cattle is based on genetics but can be changed through external influences. Main factors that predefine body composition are breed and sex of the animal. Beef breeds show higher muscle and lower body fat content than dairy breeds (Albertí et al., 2008; Pfuhl et al., 2007), while cows and heifers are reported to show higher fat content than steers and bulls (Venkata Reddy et al., 2015). The body composition of an animal can be altered by changing the genetics through selective breeding or crossbreeding (Bonilha et al., 2014; Oliveira et al., 2011), as well as by changing external influences as nutrition (Keogh, Waters, Kelly, & Kenny, 2015; McCurdy, Horn, Wagner, Lancaster, & Krehbiel, 2010). However, the proportions of body tissues in cattle also change with increasing age and live weight of the animal until maturity is reached. Hence, the growth process itself has the greatest impact on the body composition of cattle.

Owens, Dubeski, and Hanson (1993) defined growth as an increase in body tissue weight due to increasing cell proliferation and cell size enlargement. Furthermore, the authors stated that individual body tissues grow at different speeds across various stages of maturity (Owens et al., 1993). Bone tissue is described as an early developing tissue, while muscle tissue features intermediate growth, followed by fat tissue which reaches peak growth rates at the later stages of cattle growth (Augustini, Branscheid, Schwarz, & Kirchgeßner, 1992; Berg & Butterfield, 1968; Owens et al., 1993). The growth of the individual tissues is accompanied by alterations of the chemical tissue composition and thus leads to changes of the overall chemical body composition. The process of cattle growth with its progressing tissue development can best be exemplified by the alterations of tissue gain and chemical component gain during different stages of growth. Mature animals that are fed according to their maintenance requirements are supposed to have constant body composition. However, beef cattle usually are not fattened after they reach maturity but are slaughtered at empirically defined target weights when their carcasses are suitable for meat production. Hence, the feeding recommendations for beef cattle strive for ideal energy and nutrient supply to optimize cattle growth performance.

In Germany, current recommendations on energy and nutrient requirements of fattening bulls were published in 1995 (GfE, 1995). Since

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that time, continual selective breeding might have changed cattle performance as well as energy and nutrient requirements. The present study is focused on Fleckvieh (German Simmental) beef bulls. The Fleckvieh breed is a common dual-purpose cattle breed in southern Germany and provides high milk and meat yields simultaneously. Basic research on feeding recommendations for this breed was performed almost three decades ago. During the past decades, the performance potential of Fleckvieh fattening bulls has been improved by selective breeding. Hence, Fleckvieh bulls, representative for the current genetic level, feature increased frame sizes and higher body weights than bulls in past decades at the same age. This is a result of breeding Fleckvieh cows for higher milk yield and thereby increasing the cattle's body size, as shown in research by Krogmeier (2009). Furthermore, the energy requirements of Fleckvieh cattle increased with increasing frame size and milk yield. Energy requirements and energy efficiency are functions of the varying growth of different types of tissue along the growth period. Therefore, current Fleckvieh bulls may be more sensitive to variations in feed energy concentrations.

The objective of this study was to evaluate the body tissue distribution and body chemical composition, as well as the chemical composition of body tissues and composition of body weight gain of growing Fleckvieh bulls fed rations with varying energy concentrations. Through the results, a number of hypotheses were tested. The body composition and composition of weight gain of Fleckvieh bulls was expected to change during growth, showing increasing body fat content in high final weights. Furthermore, body composition and contents of gain of current Fleckvieh bulls was expected to differ from those of former times due to genetic progress. Moreover, feeding high energy rations was expected to lead to higher fat accretion and body fat content, especially in bulls with high final weights. The established hypotheses were tested based on the results of the present study.

2. Materials and methods

2.1. Animals and treatments

The experiment was conducted at the Bavarian State Research Center for Agriculture (Bayerische Landesanstalt für Landwirtschaft, LfL) according to European guidelines for animal experiments (Directive 2010/63/EU, 2010) and was approved by the ethics committee of the Ethics of Animal Experiments of LfL. In brief, 72 male Fleckvieh calves (German Simmental; age: 42 d ± 9, body weight (BW) 80 kg ±6) were randomly acquired from cattle farms in Bavaria, Southern Germany. The calves were fed with restricted amounts of milk replacer (120 g/l) and a concentrates/hay-based total mixed ration (TMR) until weaning at an average BW of 121 kg ±10 and subsequently kept on a TMR based on maize silage and concentrates for *ad libitum* intake. During the rearing phase, the feed intake of each animal group was recorded daily, and individual milk replacer intake was recorded by automatic calf feeders. Calves' BW was determined with a calf scale every second week.

The fattening period was initiated at an average BW of 225 kg ±29 and age of 154 d ± 15, when the bulls were randomly allocated to a normal energy (NE) and a high energy (HE) treatment group fed 11.6 and 12.4 MJ ME/kg DM, respectively, referring to current feeding recommendations for Fleckvieh bulls (GfE, 1995). Differences in TMRs energy concentration were reached by varying the percentage of maize silage and concentrates in the TMR for the two feeding groups. During the fattening period, the individual feed intake was recorded daily, and BW was determined using a cattle scale in four-week intervals. More details on animal treatment during calf rearing and the fattening period can be found in Honig et al. (2020).

2.2. Slaughtering and tissue sampling

Bulls from both feeding groups were slaughtered in a serial slaughter trial with final live weights of 120 kg (4 + 4 animals), 200 kg (5 + 5 animals), 400 kg (9 + 9 animals), 600 kg (9 + 9 animals), and 780 kg (9 + 9 animals), respectively. The slaughtering process was carried out at the LfL Research Abattoir in Grub, Germany, in compliance with the Council Regulation (EC) No 1099/2009 (2009) and was previously described by Honig et al. (2020). During slaughtering, the bulls' empty body weights (EBW) were determined as final live weight minus the contents of urinary bladder and gastrointestinal tract (GIT) and the whole empty body was dissected into the body tissue fractions hide, blood, organs, empty GIT, body fat, muscle, tendon, and bone.

To this effect, the blood was collected during bleeding and weighed afterwards. Dehiding was performed manually under great care to separate the hide from subcutaneous fat tissue which was supposed to remain on the carcass. After dehiding, the hide of the whole body, including hide of head and feet, was weighed, divided along the dorsal line and the right half of the hide was cut to pieces of approximately 100 cm^2 and stored at −18 °C for further processing. During evisceration, the organs (brain, eyes, spinal cord, thymus, tongue, heart, lung, diaphragm, liver with gall bladder, spleen, pancreas, kidneys, urinary bladder, testicles, penis) were collected, fat trimmed and weighed without fat trimmings. In the same way, fat tissue was manually removed from the GIT and afterwards, the GIT including its contents was weighed, emptied, washed, hung up to drain and weighed again as empty GIT. The right side of the carcass was cut to commercial beef cuts and the individual cuts were manually dissected into muscle, tendon, fat, and bone tissues. Body fat (body cavity fat, carcass fat), muscles (head, carcass, tail), tendons (carcass, feet) and bones (head, carcass, feet, tail) were weighed separately and bones of the right side of the body were stored at −18 °C for further processing. The gall bladder and urinary bladder were emptied and the organs, combined with the blood, were ground in a meat grinder (FW 114, K + G Wetter GmbH, Germany), using a 8 mm and a 2 mm punch disc. Ground tissues were homogenized using an industrial stirrer and sampled as one batch. Likewise, body fat, muscle, tendons, and GIT were ground separately in a meat grinder. Individual tissue samples were taken, and all samples were stored at −18 °C for subsequent analysis. At a later date, the hide portions were thawed in a cold storage room at 4 °C for 48 h and then homogenized using a bowl cutter (bowl volume 65 l, Krämer & Grebe, Germany). The frozen bones were crushed using a bone crusher (FX-300, Zhengzhou Fusion Machinery Equipment Co., Ltd., China) and after processing, hide and bone tissues were sampled separately and the samples stored at −18 °C.

2.3. Chemical analysis of body tissues

The frozen body tissue samples were thawed in a refrigerator at 4 °C for 48 h and thereafter homogenized in a knife mill (Grindomix GM 200, Retsch, Germany) at 5000 rpm for 1:30 min, except for hide tissue, which was already suitable for analysis after bowl cutting. Body tissues were analyzed individually for water, total ash, crude protein and ether extract contents. The water content was determined by calculating the difference in weight before and after oven drying the tissue samples at 100 °C for 16 h (VDLUFA, 2012, method 3.1). The dried samples were ashed in a muffle furnace at 550 °C for 7 h and total ash content was calculated through the difference in weight of ashed and fresh tissue (VDLUFA, 2012, method 8.1). The Dumas Method (VDLUFA, 2012, method 4.1.2) was used to determine the nitrogen content of the tissues and crude protein content was calculated as N x 6.25. The tissue samples were hydrolized with 4 N hydrochloric acid and following petroleum ether extraction in a Soxhlet extraction apparatus to determine the ether extract contents (BVL, 2014, method L 06.00–6). The energy content of each tissue was calculated based on studies of Böhme and Gädeken (1980), which determined the energy contents of ether extract and crude protein in cattle with 39.0 kJ/g and 22.6 kJ/g, respectively.

2.4. Statistical analysis and regression modelling

Statistical analysis of the body tissue composition and chemical composition of body tissues was performed using the Proc Mixed procedure of SAS (Version 9.4, SAS Institut, Cary, NC, USA) and the Kenward-Roger method to provide corrected degrees of freedom. The analysis included a two-way ANOVA with interaction (feed energy, weight group, feed energy x weight group). Differences between groups were tested using the PDIFF option with effects stated as significant when $p < 0.05$. Results are shown as LS Means (LSM) and standard error of mean (SEM). Since there were no significant effects of feed energy and feed energy x weight interaction on body tissue and chemical contents in normal and high energy treatment groups, the combined results of both animal groups are shown.

One of the aims of this study was to statistically describe the course of tissue gain in terms of type of tissue and chemical composition in bulls growing from 120 to 780 kg of body weight. In order to estimate the body composition function, we used a third order polynomial on live weight. The expected tissue growth for a given body weight is the first derivative of the body composition function for this weight. Since changes in tissue and chemical contents per kg of empty body weight may be characterized at least in part by presence of maxima or minima, the primary regression model must allow derivating such a shape of mathematical function. In contrast to *e.g.* logarithmic or exponential models, a third degree polynomial regression may fulfill this condition. Therefore, the regression analyses were based on following model:

$y_i = aLW_i + bLW_i^2 + cLW_i^3 + e_i$ (with LW = live weight, e = residual error).

The regression models did not include any intercept, because tissue matter does not exist at body weights of zero. The regression equations were calculated using Proc NLIN of SAS. Residuals of the fitted models were calculated by subtracting the predicted values of the body tissue and chemical contents of individual bulls from their observed values. The distribution of residuals was used to evaluate the goodness of fit of the regression equations, especially at the boundaries represented by the lowest and highest weight groups. A two-way analysis of variance with interaction (feed energy, weight group, feed energy x weight group) was performed with the calculated residuals. Resulting significant differences would have revealed omitted-variable bias and hence be an indicator to calculate individual models for each feeding group. No significant effect of feed x weight interaction was observed. Hence, it was statistically justified to calculate combined regression equations of both feeding groups.

To determine the model predictive performance, the coefficient of determination (R^2) was calculated for each equation as $R^2 = 1 - SSE/CSS$, where SSE was the sum of squares error and CSS the corrected sum of squares. Contents of gain were calculated using the first derivatives of the different regression equations and were scaled to 1000 g empty body weight gain (EBWG).

3. Results and discussion

3.1. Fattening performance and efficiency

The fattening performance of current dual-purpose Fleckvieh bulls was already described by Honig et al. (2020). In short, current Fleckvieh bulls showed daily weight gains of 1699 (NE) and 1792 g/d (HE) from 200 to 780 kg live weight ($p < 0.1$). In comparison, past decades Fleckvieh bulls showed an average daily gain of 1210 g/d during the 200–650 kg fattening period (Schwarz, Kirchgeßner, Augustini, & Branscheid, 1992). As a result of the inferior fattening performance, *ad libitum* fed bulls in former studies (Schwarz et al., 1992) showed higher slaughter ages at given final weights and thus reached a final weight of 600 kg approximately 130 d later than current Fleckvieh bulls. The superiority of current bulls can be further increased by feeding higher energy rations. Feeding high energy rations led to higher daily weight gains during certain stages of the fattening period and thus shortened the fattening period of 780 kg HE bulls by 21 days ($p < 0.05$; Honig et al., 2020). Hence, a superior economic efficiency can be reached by shorter production cycles of high energy fattened Fleckvieh bulls.

In terms of physiological efficiency, feed intake and energy intake per kg weight gain increased with increasing live weights of the bulls. Hence, the feed and energy efficiency of both groups decreased while the bulls increased in weight. Bulls in the lowest 80–120 kg weight range showed the best feed efficiency with 2.0 kg DM per kg weight gain, while bulls in the highest 600–780 kg weight range showed the poorest feed efficiencies with 7.0 and 7.5 kg DM per kg weight gain for NE and HE fed bulls, respectively. Comparing both energy levels, the feed efficiency of NE and HE bulls remained comparable up to high final weights at 600 kg, while thereafter HE fed bulls showed an inferior feed efficiency compared to the NE group ($p < 0.05$). Moreover, bulls in the lowest weight range showed the best energy efficiency with 24.8 MJ ME per kg weight gain, while bulls in the highest weight range showed the poorest energy efficiencies with 81.1 and 94.0 MJ ME per kg weight gain for NE and HE fed bulls, respectively. Bulls of the NE group had a significantly better energy efficiency during all stages of the fattening period and thus needed about 13 MJ less energy to gain one kg of body weight in the final fattening stage. Comparison to former research on Simmental steers and bulls done by Mandell, Gullett, Wilton, Allen, and Kemp (1998) and Sami, Augustini, and Schwarz (2004) indicates that bulls of the present study possessed an enhanced feed and energy efficiency, that can be attributed to the effect of selective breeding during the past decades.

3.2. Empty body tissue composition

Since there were no significant effects of dietary energy concentration on empty body tissue and chemical composition in normal and high energy treatment groups, the combined results of both animal groups are shown. Empty body weights of weight groups 120, 200, 400, 600, and 780 kg were 104, 176, 370, 553, and 734 kg, respectively. The average empty body tissue composition of bulls in different weight groups is displayed in Table 1. The results were compared to recalculated empty body tissue compositions of *ad libitum* fed Fleckvieh bulls with 200–650 kg live weight, based on data by Schwarz & Kirchgessner, 1991, Augustini et al. (1992) and Otto et al. (1994). For this purpose, a relation of empty body weight to live weight of 0.88 for 200 kg bulls and 0.93 for 400–780 kg bulls was assumed as inferred from present data. Limitations in comparability are caused by dissimilarities in tissue collection methods during slaughtering and carcass processing. Muscle tissue was the largest fraction of the bulls' empty bodies. In the present study, muscle tissue and tendon tissue percentage remained constant in all weight groups at an average of 42.9% and 4.2%, respectively. These findings agree with data of former studies, which revealed muscle and

Table 1
Average empty body tissue composition of bulls in different weight groups.

Empty body tissues	Weight group					SEM	*p*-value
	120 kg $n = 8$	200 kg $n = 10$	400 kg $n = 18$	600 kg $n = 18$	780 kg $n = 18$		weight
Hide (%)	9.2^{A}	10.9^{BD}	11.9^{C}	11.2^{B}	10.5^{D}	0.19	<0.0001
Blood (%)	6.0^{A}	5.3^{B}	4.9^{C}	4.6^{D}	4.0^{E}	0.13	<0.0001
Organs (%)	7.2^{A}	7.2^{A}	6.5^{B}	6.0^{C}	5.7^{D}	0.12	<0.0001
GIT (%)	7.4^{A}	7.0^{A}	5.7^{B}	4.4^{C}	3.9^{D}	0.16	<0.0001
Fat (%)	3.7^{A}	6.8^{B}	10.1^{C}	14.1^{D}	18.6^{E}	0.57	<0.0001
Muscle (%)	43.3	42.6	43.1	43.1	42.2	0.51	0.4332
Tendon (%)	4.2	4.1	4.3	4.2	4.1	0.10	0.3653
Bone (%)	19.0^{A}	16.1^{B}	13.5^{C}	12.4^{D}	11.0^{E}	0.18	<0.0001

Means within a row sharing the same superscript are not significantly different.

tendon shares of 41% and 3%, respectively (Augustini et al., 1992). Furthermore, past decades' research indicated an increase of fat tissue proportion during the fattening period from 7 to 15% in 200–650 kg bulls (Augustini et al., 1992; Otto et al., 1994; Schwarz & Kirchgessner, 1991). This is in line with results of the present study, which showed fat tissue percentages of 6.8–14.1% in 200–600 kg bulls. In total, the amount of fat tissue in the bull's empty bodies increased from the lowest to the highest weight group by 14.9%. In contrast to this, bone, GIT, blood and organ tissues decreased by 8.0, 3.5, 2.0 and 1.5%, respectively ($p < 0.05$). For bone tissue, authors of experiments from past decades reported a decrease from 12 to 9% in 200–650 kg bulls (Augustini et al., 1992), whereas the present research revealed a decrease from 16.1–12.4% in the 200–600 kg weight range. Differences in bone tissue proportion might occur because only carcass bones were considered in the former study and thus bones of the feet and head were not taken into account, while they were completely collected in the present study. Furthermore, blood and organ tissue proportions are not fully comparable to former research because in those studies not all organs were collected, and the amount of blood was not specified. However, similarities in tissue share were evident in GIT tissue, which was specified by Otto et al. (1994) as a decrease from 7 to 4% in 200–650 kg bulls, while the present study reports a decrease of GIT tissue proportions from 7.0–4.4% in 200–600 kg bulls. In contrast to the tissues which showed either a constant increase or a constant decrease of tissue share, the amount of hide tissue increased from 9.2–11.9% in 120–400 kg bulls and then decreased by 1.4% to 10.5% in the highest weight group ($p < 0.05$). Data from former studies indicated a hide percentage at an average of 9% (without hide of the head) with minor variations during growth (Otto et al., 1994). The comparison with former studies covering the same breed reveals that the empty body tissue distribution in current bulls and *ad libitum* fed bulls of former studies at defined final weights has not changed during the past decades. These findings suggest that body composition within breed and sex depends on body weight rather than age.

Furthermore, present data confirm the model of specific tissue development processes at different stages of growth (Augustini et al., 1992; Berg & Butterfield, 1976; Owens et al., 1993). Since a functional skeletal system is mandatory for the calf from day one of life, the amount of bone tissue decreases during growth while other tissues reach their peak of development. Individual organs develop during different stages of cattle growth and the GIT is subject to changes since it has to adjust to roughage digestion after weaning. The decrease of organ, blood, GIT and bone tissue proportions are associated with an increase of fat tissue proportion. Fat tissue is described as a late developing tissue (Augustini et al., 1992; Berg & Butterfield, 1976; Owens et al., 1993) and functions as energy storage for periods of energy shortage.

3.3. Chemical composition of the empty body and body tissues

The chemical contents and related regressions are illustrated in Fig. 1. It is noticeable that the chemical composition of the animals within the respective weight group is very similar and was not changed by feeding varying energy concentrations. The greatest proportion of the bull's empty bodies in all weight groups consisted of water (Table 2). During growth, the amount of body water in the empty bodies of Fleckvieh bulls decreased by 13.1%, while ether extract increased by 15.1% ($p < 0.05$). Present data showed ether extract percentages of 10.2–17.5% for 200–600 kg bulls, which agree widely with data of Kirchgessner, Schwarz, Otto, Reimann, and Heindl (1993), reporting ether extract shares of 8.3–16.2% in 200–650 kg *ad libitum* fed bulls. The shifts in the distribution of water and ether extract in cattle at different final weights are consistent with findings of former studies (Buckley, Baker, Dickerson, & Jenkins, 1990; Carstens, Johnson, Ellenberger, & Tatum, 1991; Kirchgessner et al., 1993; McCurdy et al., 2010; Schulz, Oslage, & Daenicke, 1974). As a side effect of the increasing amount of ether extract, the energy content of the bulls' empty body tissues increased significantly from the lowest to the highest weight group by 5.5 MJ/kg EBW. Present data revealed an energy content ranging from 8.3–11.1 MJ/kg in 200–600 kg bulls, which is in agreement with data of Kirchgessner et al. (1993), which indicated an increase in energy content from 7.8–10.8 MJ/kg in 200–650 kg bulls. Concerning the amounts of crude protein in the bull's empty bodies, the percentage of crude

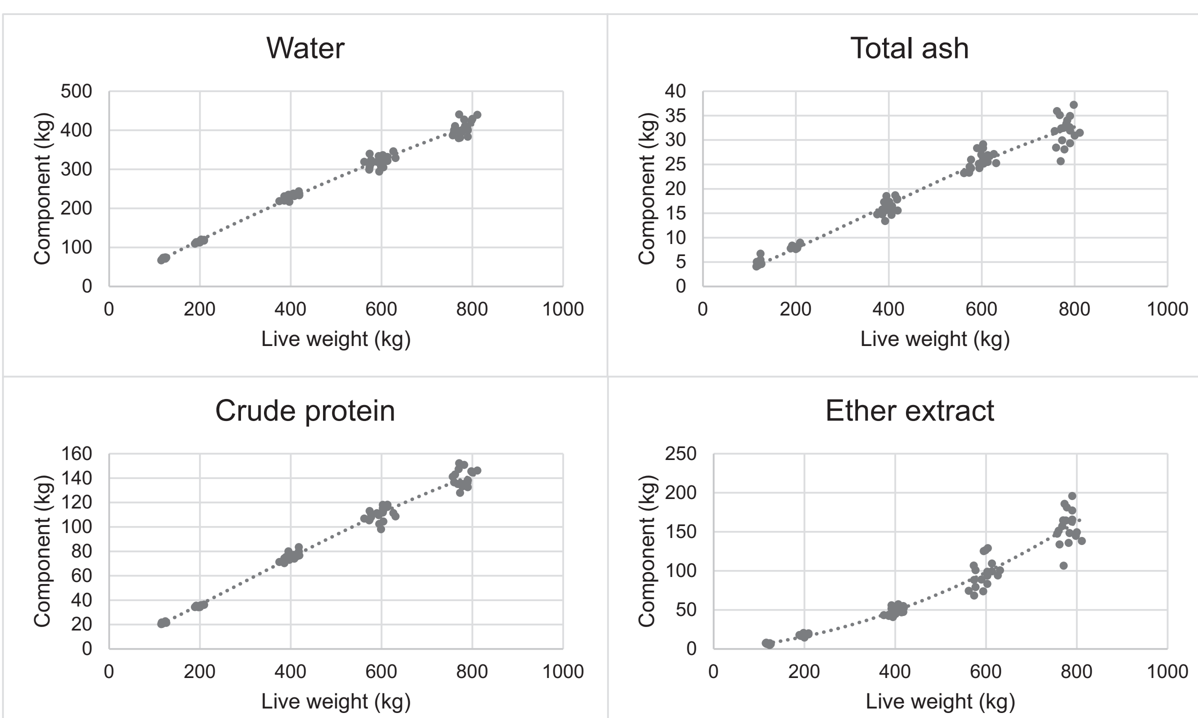

Fig. 1. Chemical body components of bulls with different live weights.

Table 2
Average energy and chemical composition of the bull's empty body and body tissues in different weight groups.

Empty body composition	Weight group					SEM	p-value
	120 kg n = 8	200 kg n = 10	400 kg n = 18	600 kg n = 18	780 kg n = 18		weight
Empty body							
Water (%)	68.4^{A}	65.2^{B}	62.1^{C}	58.1^{D}	55.3^{E}	0.51	<0.0001
Total ash (%)	4.8^{A}	4.6^{AB}	4.4^{B}	4.6^{A}	4.4^{B}	0.10	0.0079
Crude protein (%)	20.6^{A}	20.0^{AB}	20.5^{A}	19.8^{B}	19.1^{C}	0.20	<0.0001
Ether extract (%)	6.2^{A}	10.2^{B}	13.0^{C}	17.5^{D}	21.3^{E}	0.67	<0.0001
Energy (MJ/kg)	6.9^{A}	8.3^{B}	9.5^{C}	11.1^{D}	12.4^{E}	0.22	<0.0001
Hide							
Water (%)	67.3^{A}	67.2^{A}	63.1^{B}	60.6^{C}	58.7^{D}	0.56	<0.0001
Total ash (%)	0.8^{A}	0.7^{B}	0.7^{C}	0.6^{D}	0.6^{D}	0.02	<0.0001
Crude protein (%)	30.5^{A}	29.7^{A}	33.2^{B}	33.7^{B}	34.3^{B}	0.56	<0.0001
Ether extract (%)	1.4^{A}	2.4^{AB}	3.0^{B}	5.1^{C}	6.4^{D}	0.48	<0.0001
Energy (MJ/kg)	7.4^{A}	7.7^{A}	8.7^{B}	9.6^{C}	10.2^{D}	0.17	<0.0001
Organs & Blood							
Water (%)	77.3^{A}	75.1^{AB}	73.6^{BC}	73.0^{BC}	72.7^{C}	0.72	0.0007
Total ash (%)	1.0	1.0	1.0	1.0	1.0	0.02	0.2525
Crude protein (%)	16.6^{A}	16.5^{A}	17.0^{A}	17.6^{B}	17.8^{B}	0.20	<0.0001
Ether extract (%)	5.1^{A}	7.4^{AB}	8.4^{B}	8.4^{B}	8.6^{B}	0.77	0.0343
Energy (MJ/kg)	5.7^{A}	6.6^{AB}	7.1^{B}	7.2^{B}	7.4^{B}	0.29	0.0038
Gastrointestinal tract							
Water (%)	81.0^{A}	76.9^{B}	74.7^{B}	74.2^{BC}	71.8^{C}	0.99	<0.0001
Total ash (%)	1.2^{AB}	1.2^{AB}	1.2^{AB}	1.1^{A}	1.3^{B}	0.06	0.2093
Crude protein (%)	12.8^{A}	12.9^{A}	11.7^{B}	11.6^{B}	11.3^{B}	0.30	0.0010
Ether extract (%)	5.0^{A}	9.0^{A}	12.4^{B}	13.1^{BC}	15.6^{C}	1.16	<0.0001
Energy (MJ/kg)	4.8^{A}	6.4^{B}	7.5^{BC}	7.8^{CD}	8.6^{D}	0.41	<0.0001
Fat							
Water (%)	49.3^{A}	30.1^{B}	20.6^{C}	17.4^{D}	15.7^{D}	0.86	<0.0001
Total ash (%)	0.6^{A}	0.4^{B}	0.2^{C}	0.2^{CD}	0.2^{D}	0.01	<0.0001
Crude protein (%)	11.2^{A}	7.3^{B}	7.0^{B}	6.0^{BC}	5.6^{C}	0.52	<0.0001
Ether extract (%)	39.0^{A}	62.3^{B}	72.2^{C}	76.4^{D}	78.6^{D}	1.10	<0.0001
Energy (MJ/kg)	17.7^{A}	25.9^{B}	29.7^{C}	31.1^{D}	31.9^{D}	0.37	<0.0001
Muscle							
Water (%)	75.8^{A}	75.6^{A}	74.9^{B}	73.6^{C}	73.5^{C}	0.23	<0.0001
Total ash (%)	1.1^{A}	1.0^{B}	1.0^{B}	1.0^{B}	1.0^{B}	0.01	0.0041
Crude protein (%)	21.5	21.1	21.4	21.3	21.1	0.15	0.3516
Ether extract (%)	1.6^{A}	2.3^{AB}	2.7^{B}	4.1^{C}	4.4^{C}	0.21	<0.0001
Energy (MJ/kg)	5.5^{A}	5.6^{A}	5.9^{B}	6.4^{C}	6.5^{C}	0.08	<0.0001
Tendon							
Water (%)	60.9^{A}	57.7^{B}	54.2^{C}	52.0^{D}	49.2^{E}	0.76	<0.0001
Total ash (%)	0.8^{A}	0.7^{AB}	0.7^{AB}	0.7^{AB}	0.6^{B}	0.05	0.1414
Crude protein (%)	25.9^{A}	26.0^{A}	23.6^{B}	23.2^{B}	23.6^{B}	0.55	0.0009
Ether extract (%)	12.4^{A}	15.6^{A}	21.6^{B}	24.1^{BC}	26.6^{C}	1.10	<0.0001
Energy (MJ/kg)	10.7^{A}	11.9^{B}	13.7^{C}	14.6^{D}	15.7^{E}	0.34	<0.0001
Bone							
Water (%)	46.9^{A}	40.6^{B}	39.2^{B}	32.3^{C}	30.7^{C}	0.85	<0.0001
Total ash (%)	21.0^{A}	23.8^{B}	26.8^{C}	31.6^{D}	33.1^{D}	0.76	<0.0001
Crude protein (%)	20.0^{A}	20.4^{A}	22.0^{B}	21.6^{B}	21.9^{B}	0.29	<0.0001
Ether extract (%)	12.1^{AC}	15.2^{B}	12.0^{C}	14.6^{B}	14.3^{AB}	0.73	0.0043
Energy (MJ/kg)	9.2^{A}	10.5^{B}	9.6^{A}	10.6^{B}	10.5^{B}	0.26	0.0008

Means within a row sharing the same superscript are not significantly different.

protein decreased during growth by 1.5%, which is in agreement with data of Schulz et al. (1974) and Buckley et al. (1990), while the amount of total ash decreased slightly from the lowest to the highest weight group by 0.4% ($p < 0.05$). Contrary to these findings, Kirchgessner et al. (1993) reported no significant changes in crude protein and total ash content in the empty bodies of *ad libitum* fed bulls of different weights. The authors reported crude protein content from 20.2–20.0% and total ash content from 4.3–4.2% in bulls of 200–650 kg live weight, which are comparable to data of the present research in the corresponding weight range.

Formerly published research of Ferrell and Jenkins (1998) on the chemical empty body composition of *ad libitum* fed beef steers of different crossbreeds at about 500 kg live weight indicated an empty body water content of 50.2–54.0%, while variations in ether extract content (25.7–30.8%) were greater than in crude protein (13.8–15.1%) and total ash showed the least variation from 5.0–5.3%. These findings agree with data of Basarab et al. (2003) which measured an empty body composition of 51.7% body water, 27.7% ether extract, 16.5% protein and 4.1% ash in crossbreed beef steers with 502 kg live weight. In contrast, Wright and Russel (1991) reported the empty body composition of high energy fed 450 kg crossbreed beef steers to be 61.2% water, 15.8% fat, 19.0% protein and 4.0% ash and thus outline a lower ether extract, but higher body water and crude protein content of their steers, which corresponds widely with the results of the present study. Variations in chemical empty body composition of steers in the discussed studies may occur due to differences in cattle breed, sex, and feed, as well as differences in tissue sampling and preparation. Steers feature higher empty body and carcass ether extract contents (Kirchgessner et al., 1993). Research on steers also indicated higher muscle lipid concentration (Schreurs et al., 2008) and higher carcass fatness scores (Nogalski et al., 2014) compared to bulls. Differences in fat content of bulls and steers increased with the live weights of the animals (Kirchgessner et al., 1993; Nogalski et al., 2014; Schreurs et al., 2008).

The changes in chemical empty body composition of growing bulls are caused by progressive development and thus changes in chemical composition of the individual body tissues. The greatest change in tissue composition could be observed in the bull's body fat tissue. The ether extract content in fat tissue ranged from 39.0–78.6% from the lowest to the highest weight group and thus increased by 39.6%, while the water and crude protein content decreased by 33.6 and 5.6%, respectively ($p < 0.05$). The increase of ether extract percentage at the expense of water and crude protein in the fat tissue of growing bulls is in agreement with data of Schulz et al. (1974), Berg and Butterfield (1976) and Otto et al. (1994) and illustrates progressive maturing of the animals.

In contrast to the other tissues, the maturing of bone tissue was characterized by 12.1% increase of total ash from 120 to 780 kg live weight, which indicates progressive mineralization and ossification of the bones. These findings are in line with results of Reimann, Otto, Schwarz, and Kirchgessner (1993) which reported 10% increase of total ash in bone tissues of 200–650 kg fattening bulls. Bone tissue comprised the highest amount of minerals containing total ash compared to the other body tissues, as was previously reported by Schulz et al. (1974).

In terms of crude protein content, bone tissue is comparable to muscle tissue which was the only tissue whose crude protein content did not change during growth but remained constant at an average of 21.3%. These findings agree with data of Schulz et al. (1974) and Reimann et al. (1993), who reported an average crude protein content of 20% and 21.9% in muscle tissue of growing beef bulls, respectively.

As previously described, fat tissue showed the greatest decrease of crude protein contents from the lowest to the highest weight group, while on the other hand hide tissue revealed the greatest increase of crude protein content by 3.8%, which is in line with results of Schulz et al. (1974). However, the increase of crude protein content in hide tissue was not confirmed in previous research by Otto et al. (1994), which reported an average crude protein content of 31% in hide tissue of 200–650 kg fattening bulls. In addition, Otto et al. (1994) indicated a constant crude protein percentage of GIT tissue in growing *ad libitum* fed bulls, which is in contrast to results of the present study where the amount of crude protein in the GIT tissue decreased during growth by 1.5% ($p < 0.05$). Additionally, the water content of GIT tissue decreased by 9.2% while the amount of ether extract increased by 10.6% ($p < 0.05$). Hence, GIT tissue reflects major points of tissue development in growing cattle, including an increase in ether extract at the expense of water and crude protein and thus, an increase of energy content in all body tissues.

3.4. Composition of body weight gain

Calculated regression equations for body tissues and chemical components are displayed in the supplementary material. Since the analysis of variance of the residuals showed no significant effects of the dietary energy concentration on body tissues and chemical components, the combined results of both animal groups are shown. All models show a very good fit, as described by the coefficient of determination. The first derivative of each regression equation was used to calculate the tissue and chemical component gain per kg EBWG over a range of live weights.

Gains of blood, organ, GIT, and bone tissues constantly decreased from the lowest to the highest estimated live weight (Table 3, Fig. 2), where the early developing bone tissue showed the greatest decrease of 84 g/kg EBWG. Intermediately developing tissues such as hide, muscle and muscle associated tendon displayed an increase of the estimated tissue gain up to a peak at 300 kg live weight and a decrease in gain afterwards. The decrease in tissue gain of early and intermediately developing tissues is accompanied by a strong increase of late developing fat tissue gain, which increased by 334 g/kg EBWG between 100 and 800 kg live weights.

The content of chemical components per kg EBWG (Table 3, Fig. 3) was dominated by body water in all weight groups, as was previously reported by Kirchgessner, Schwarz, Reimann, Heindl, and Otto (1994). The loss in water as live weight increased is in agreement with Schulz et al. (1974) and was also described by Kirchgessner et al. (1994), who observed a decrease of water content in growing *ad libitum* fed bulls.

The amount of water is directly related to protein decline. Former studies on *ad libitum* fed Fleckvieh bulls showed protein content, of 175 g/kg BWG in 200–350 kg bulls, 175 g/kg BWG in 350–500 kg bulls and 206 g/kg BWG in 500–650 kg bulls (Schwarz, 1995; Schwarz, Kirchgessner, & Heindl, 1995) and thus an increase of protein content towards the end of the fattening period. Assuming a mean relation of EBWG to BWG of 0.95 as derived from the present study and also assumed by GfE (1995), this corresponds to respective protein content values of 184 g/kg EBWG in 200–350 kg bulls, 184 g/kg EBWG in 350–500 kg bulls and 217 g/kg EBWG in 500–650 kg bulls. In contrast, crude protein content of bulls in the present study decreased during growth from 206 to 177 g/kg EBWG as liveweight increased from 200 to 600 kg. A decreasing protein content was also reported for Schwarzbunte (an ancient dual-purpose breed) bulls in studies by Schulz et al. (1974). The authors indicated a lower protein content of 160–110 g/kg BWG throughout the 175–575 kg live weight range.

Furthermore, data of Schulz et al. (1974) exhibited a rapid increase of ether extract gain per kg BWG, ranging from 70 to 500 g/kg BWG over the 175–575 kg live weight range and thus showed a lower fat content at the beginning of the fattening period but higher fat content at higher final weights, compared to bulls of the present study. These observations are consistent with historical reports on Fleckvieh bulls, which featured ether extract content of 163 g/kg BWG in 200–350 kg bulls up to 207 g/kg BWG in 500–650 kg bulls (Schwarz, 1995; Schwarz et al., 1995).

Table 3
Calculated average body tissue, chemical composition, and energy contents per kg empty body weight gain of bulls at different live weights.

Empty body weight and composition of gain	Live weight							
	100 kg	200 kg	300 kg	400 kg	500 kg	600 kg	700 kg	800 kg
Empty body weight (kg)	87	178	272	367	463	560	657	752
Body tissue gain								
Hide (g/kg EBWG)	112	119	120	117	109	96	77	52
Blood (g/kg EBWG)	54	50	46	42	36	30	23	14
Organs (g/kg EBWG)	71	64	58	54	50	47	44	42
GIT (g/kg EBWG)	70	51	37	27	19	15	13	13
Fat (g/kg EBWG)	62	98	136	177	222	272	330	396
Muscle (g/kg EBWG)	429	436	438	435	427	415	397	374
Tendon (g/kg EBWG)	42	44	44	43	42	39	36	31
Bone (g/kg EBWG)	161	138	120	105	94	86	80	77
Chemical component gain								
Ether extract (g/kg EBWG)	89	133	174	214	254	294	335	379
Crude protein (g/kg EBWG)	204	206	204	198	190	177	161	140
Total ash (g/kg EBWG)	44	47	48	47	46	42	38	32
Water (g/kg EBWG)	662	614	574	540	511	487	466	448
Energy (MJ/kg EBWG)	8.1	9.8	11.4	12.8	14.2	15.5	16.7	18.0

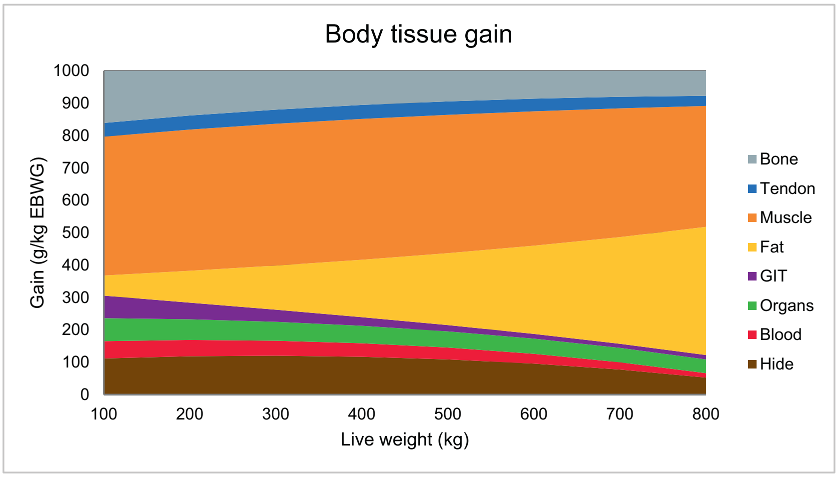

Fig. 2. Calculated body tissue gain per kg empty body weight gain.

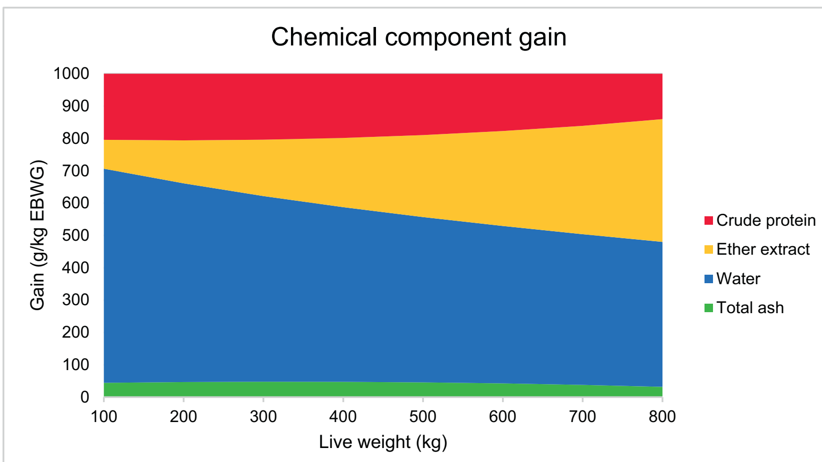

Fig. 3. Calculated chemical component gain per kg empty body weight gain.

However, reported historical content of fat in bulls of high final weights were lower than those of current bulls in the same weight range. Ether extract content increased at higher final weights mainly at the expense of water, which corresponds to the previously described changes to chemical empty body composition and is associated with fat tissue development, which increases during cattle growth. However, ether extract content did not exceed the content of water during any stage of growth, which agreed with data from *ad libitum* fed bulls (Kirchgessner et al., 1994).

The increase of ether extract gain in the course of growth was associated with an increase in energy content, ranging from 9.8–18.0 MJ/kg EBWG in 200–800 kg bulls during the fattening period. Previous research on bulls of the same breed showed energy contents of 10.3 MJ/kg BWG in 200–350 kg bulls, 10.8 MJ/kg BWG in 350–500 kg bulls and 12.7 MJ/kg BWG in 500–650 kg bulls (Schwarz, 1995; Schwarz et al., 1995). Hence, current bulls feature comparable energy contents in the beginning of the fattening period, but higher energy contents in the mid and at end of the fattening period. This may lead to higher energy requirements compared to the recommendations given by GfE (1995) if the same maintenance requirements and the same retention factors for ME are assumed.

In contrast, the gain of total ash per kg EBWG was subject to minor changes, as total ash content slightly increased until it reached a peak at 300 kg live weight and subsequently decreased at higher weight. These shifts in total ash content are consistent with data of Schulz et al. (1974), who observed a strong decrease of ash content in high final weights, with 45 g/kg BWG in 370–480 kg bulls compared to 27 g/kg BWG in 480–576 kg bulls.

Overall, the changes in chemical component gain per kg EBWG are characterized by an increase of ether extract at the expense of water and subsequent crude protein, while total ash content remained at a relatively constant low level and thus reflected the previously described changes to the chemical body composition during cattle growth.

3.5. General discussion

The research project aimed at analyzing the changes in body composition during cattle growth. The largest fraction of the bulls' empty bodies consisted of muscle tissue, the crude protein proportion of which remained constant throughout all weight groups. The first step of muscle growth takes place prenatally, when the number of muscle fibers increases (hyperplasia) and is established before birth (Greenwood, Hunt, Hermanson, & Bell, 2000; Hocquette, 2010). During postnatal growth, muscle fibers increase in size and diameter (hypertrophy) and changes in fiber types occur (Picard & Gagaoua, 2020). Hence, a constant protein content may be required to enable muscle function and the frequent reorganization of the muscle fibers during the bull's growth. Other tissues rich in protein are hide, tendon and bone tissue. The protein proportion of hide and bone tissue increased significantly during growth, while tendon tissue showed a decrease of protein percentage.

The decreasing amount of protein may not be attributed to increasing fat storage in tendon tissue, but to the anatomical connection of fat and tendon tissues when dissecting slaughtered animals into tissue fractions.

The gain of protein rich tissues decreased during the cattle growth process, which was also associated with a decrease in crude protein gain per kg EBWG. In contrast, fat tissue and associated ether extract gain increased during growth. The increasing fat tissue proportion is an effect of the increasing fat cell number and size, as described by Robelin (1981). The proportion of ether extract in the fat tissue increased with increasing live weight of the animals. Besides ether extract, fat tissue also contains a high amount of water and protein rich connective tissue as is obvious in early stages of fat tissue development. The connective tissue helps to structure the individual fat tissues within the animal's body. An increase of ether extract at the reduction of water was obvious in all body tissues and therefore represents an essential aspect of animal growth.

Another important part of the research project was the influence of dietary energy concentration on cattle growth performance, body composition and rates of gain. Indeed, a serial slaughter trial at defined chronological age (*e.g.* days on fattening) might have shown progressively growing differences in body composition of high energy *vs.* normal energy fed bulls due to higher daily weight gains. This trial, however, was designed for body composition measurements at specific weight groups in order to identify patters of tissue growth at comparable stages of physiological maturity. Interestingly, high energy rations did not alter the body composition or composition of gain of growing Fleckvieh bulls. High energy fed bulls converted feed energy efficiently into growth up to the highest observed weight group (780 kg), which is evident from the high growth rates at constant composition of empty body weight gain.

The increased growth potential of Fleckvieh bulls is a result of ongoing selective breeding for fitness, milk, and beef traits during the past decades. The weighting of Fleckvieh trait complexes for the calculation of the total merit index is specified in the annual report from the Association of Austrian Cattle Breeders (Kalcher, 2015). According to the report, primary focus of breeding Fleckvieh cattle are fitness traits (*e.g.* health, fertility, longevity) and milk traits (fat and protein yield) with 44 and 38% of the total merit index, respectively. Beef traits as daily live weight gain, dressing percentage and carcass grade account for 18% of the total merit index (Kalcher, 2015). Hence, breeding for beef traits is an integral part of the breeding of Fleckvieh cattle and led to bulls with increased fattening and slaughter performance.

The increased performance potential of current Fleckvieh bulls allows fattening to high final weights as 750 kg, which are already common at the Bavarian meat market (LKV, 2020). The feed efficiency (feed intake in kg DM per kg weight gain) of Fleckvieh bulls increased during the past decades, which can be explained by the higher daily weight gain of current bulls up to high final weights. Furthermore, bulls in high weight groups feature better carcass and meat quality traits, as already shown in studies by Honig et al. (2020). On the other hand, the feed efficiency decreases with increasing age of the animals, which is related to the higher fat accretion in high weight groups. Moreover, cattle handling facilities and slaughterhouse equipment must be adapted to the increased weight and size of the animals. All in all, fattening Fleckvieh bulls to high final weights can be recommended if the structural conditions allow it.

The fattening up to high final weights makes it necessary to have reliable recommendations on energy and nutrient requirements of growing bulls. The most recent feeding recommendations for Fleckvieh cattle cover a weight range from 175 to 625 kg live weight (GfE, 1995) and thus do not cover high final weights, which are already common at the Bavarian meat market. Hence, feeding recommendations for bulls above the specified weight range are currently calculated by extrapolation, which does not necessarily reflect the requirements of the animals. The present research shows that protein accretion decreases, while energy accretion increases with increasing live weight of the bulls. Consequently, the requirements for protein in relation to energy decrease during cattle growth. For this reason, phase feeding for growing bulls should be considered to feed the bulls close to their protein requirements and reduce nitrogen excretions due to protein oversupply. The combination of phase feeding and adjusted recommendations for protein and energy requirements can contribute to a sustainable feeding strategy for growing Fleckvieh bulls.

4. Conclusion

The results of the present study allow an evaluation of the hypotheses formulated in the introduction. The hypothesis that feeding high energy rations to current Fleckvieh bulls leads to higher body fat content and higher ether extract content per kg weight gain was disproved by the results of our research. Our results show that feeding very high dietary energy concentrations did not alter the body composition or composition of gain at a given weight to a relevant extent. Hence, the maximum performance potential did not seem to be exploited by our high energy ration. On the other hand, feeding lower energy concentrations can reduce the amount of feed energy required for a certain weight gain, although at the expense of a longer fattening period.

A hypothesis confirmed by the results of the present study was that the bulls body composition changes during the growth process. As expected, the amount of fat per kg of gain increased with increasing live weight at the expense of muscle growth. Although the amount of protein per kg gain decreases only moderately, the feed energy required for a certain gain increases by more than 100% from early to later stages. Our results confirm that bulls were not yet fully grown in the highest weight group. Thus, a further increase of fat tissue and ether extract content can be expected until bulls are completely mature.

Furthermore, the hypothesis that body composition of current Fleckvieh bulls differs from those of former times bulls was disproved by the results of the present study. The comparison with former studies covering the same breed indicates that the empty body tissue distribution of current Fleckvieh bulls and *ad libitum* fed former bulls with the same final weights has not changed considerably during the past decades. These findings suggest that body composition depends on body weight (stage of relative maturity) rather than age.

However, current Fleckvieh bulls showed an enhanced performance potential and featured lower crude protein contents, combined with higher ether extract and energy contents per kg gain in high final weights. The ratio of metabolizable protein relative to energy decreased with increasing live weight of the animals. Therefore, the crude protein content of the rations should be reduced during fattening to avoid unnecessary nutrient excretion. In summary, the present research project showed that a combination of phase feeding and adjusted recommendations on protein and energy requirements can contribute to a more sustainable feeding strategy for growing Fleckvieh bulls.

Declarations of interest

None.

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CRediT authorship contribution statement

Aniela C. Honig: Investigation, Data Curation, Formal analysis, Writing-Original Draft. **Vivienne Inhuber**: Investigation, Writing-Review & Editing. **Hubert Spiekers**: Resources, Supervision, Writing-Review & Editing. **Wilhelm Windisch**: Conceptualization, Writing-Review & Editing. **Kay-Uwe Götz**: Funding acquisition, Writing-

Review & Editing. **Manfred Schuster**: Formal analysis, Validation, Data curation. **Thomas Ettle**: Conceptualization, Methodology, Supervision, Project administration, Writing-Review & Editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.meatsci.2021.108685.

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