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Assessment of body composition and allometric growth of body tissues and nutrients in Fleckvieh bulls fed rations with varying energy concentrations

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Table of Contents

List of Publications

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Abstracts and articles in conference proceedings

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List of Abbreviations

a*	redness
aNDFom	neutral detergent fiber with amylase solution and without residual ash
ANOVA	analysis of variance
b*	yellowness
BW	body weight
BWG	body weight gain
°C	degree Celsius
Ca	calcium
CA	crude ash
CF	crude fat
cm	centimeter(s)
cm^2	square centimeter(s)
CP	crude protein
d	day(s)
DLG	German Agricultural Society
DM	dry matter
e	residual error
EBW	empty body weight
EBWG	empty body weight gain
EC	European Commission
g	gram(s)
GfE	Society of Nutrition Physiology
GIT	gastrointestinal tract
h	hour(s)
HE	high energy treatment group
IMF	intramuscular fat
kg	kilogram(s)
kJ	kilojoule
L	liter(s)
L*	lightness
LfL	Bavarian State Research Center for Agriculture

LS	least square
LSM	least square means
LT	longissimus thoracis muscle
LW	live weight
ME	metabolizable energy
min	minute(s)
MIXED	mixed model procedure in SAS
MJ	megajoule
N	nitrogen or newton
n	number of individuals per treatment group
NE	normal energy treatment group
NLIN	nonlinear procedure in SAS
P	phosphorus
p	probability of error
PDIFF	pairwise difference option of the mixed model procedure in SAS
pH	negative decadic logarithm of the hydrogen ion concentration in a solution
R^2	coefficient of determination
rpm	revolutions per minute
SAS	Statistical Analysis System
SE	standard error
SEM	standard error of mean
TMR	total mixed ration
VDLUFA	Association of German Agricultural Analytic and Research Institutes

List of Figures

List of Tables

Summary

This doctoral thesis generates basic data to determine the nutrient and energy requirements of growing Fleckvieh (German Simmental) beef bulls under different feeding regimes. Hence, analyses of body composition and nutrient and energy accretion rates were performed in growing Fleckvieh bulls fed rations with different energy concentrations. The results illustrate allometric growth patterns in cattle and demonstrate how more sustainable feeding concepts can be realized.

Seventy-two Fleckvieh bull calves, representing the current genetic level, were customarily reared. During the fattening period, the calves were allocated to normal energy and high-energy treatment groups fed 11.6 and 12.4 megajoule metabolizable energy per kilogram dry matter, respectively. Differences in dietary energy concentrations were achieved by varying the amounts of concentrates and maize silage in the feeding rations. Bulls from both feeding groups were slaughtered in a serial slaughter trial at final live weights of 120, 200, 400, 600, and 780 kilograms. During slaughter and subsequent beef cutting, the bulls' bodies were dissected into individual tissue fractions, which were homogenized and analyzed for their chemical composition. Regression modeling was applied to determine the body composition of the growing bulls. The first derivative of the individual equations was used to calculate the gain composition and describe changes in body proportions throughout the growth process.

The study results are presented in two publications. The first publication specifies fattening and slaughter performance in current Fleckvieh bulls at defined final weights and under feeding regimes with varying energy concentrations. The results demonstrate that Fleckvieh bulls at the current genetic level feature increased growth potential and final weights, compared to Fleckvieh bulls in previous decades. Current Fleckvieh bulls efficiently exploited energy and nutrients in the offered feed and exhibited increased daily weight gains, leading to high final weights. High-energy fed bulls showed increased growth performance compared to bulls fed a regular-energy diet. Differences in carcass composition and meat quality traits in growing bulls from both treatment groups were not recorded. Consequently, Fleckvieh bulls fed rations with lower energy concentrations needed more time to reach the highest target weight. However, slaughter performance and meat quality traits were comparable to those of bulls fed high-energy diets.

The second publication assesses body tissue composition, body chemical composition, and the composition of body weight gain in growing Fleckvieh bulls fed rations with varying energy concentrations. The results indicate that feed containing varying amounts of energy did not alter body composition or energy and nutrient accretion rates in growing Fleckvieh beef bulls. During growth, unequal changes in body tissue gain and nutrient accretion, attributable to allometric cattle growth, became apparent. Comparison with earlier research reveals that current Fleckvieh bulls with high live weights feature lower rates of crude protein accretion but higher crude fat and energy accumulation rates than bulls in previous decades. Hence, feeding recommendations for growing Fleckvieh bulls must be regularly adjusted to suit energy and nutrient requirements and increase daily weight gain and target weights.

In summary, growing Fleckvieh bulls in the normal and high-energy feed intake groups demonstrated similar body composition, carcass composition, composition of gain, and meat quality traits. It can be concluded that feeding high-energy rations is not necessary from a metabolic standpoint. Fleckvieh bulls can be fattened using lower energy, roughage-rich rations according to their physiological advantages as ruminants, which also contributes to animal welfare. Future feeding concepts should aim to increase roughage feeding in cattle nutrition to reduce competition for resources used in livestock feed and human food production. Furthermore, phase feeding should be used to feed growing cattle according to their energy and nutrient requirements and reduce nitrogen excretion and the resulting environmental impacts. Hence, more sustainable cattle feeding concepts can contribute to resource conservation, environmental protection, and increased animal welfare.

Zusammenfassung

Ziel des Promotionsprojektes war es, eine Datengrundlage für die Ermittlung des Nährstoff- und Energiebedarfs wachsender Fleckvieh Mastbullen bei unterschiedlichen Fütterungsbedingungen zu generieren. Zu diesem Zweck wurden die Körperzusammensetzung und der Nährstoff- und Energieansatz wachsender Fleckviehbullen bei Fütterung mit unterschiedlichen Energiegehalten analysiert. Anhand der Ergebnisse konnten typische Muster des allometrischen Wachstums in Rindern dargestellt werden. Außerdem wurde gezeigt, wie nachhaltigere Rinder-Fütterungskonzepte realisiert werden können.

Für die Studie wurden 72 Fleckviehbullenkälber, repräsentativ für das aktuelle genetische Material, zunächst einheitlich entsprechend gängiger Praxis mit Milchaustauscher und Kälberrationen aufgezogen. Anschließend wurden die Tiere für den Mastzeitraum in zwei Fütterungsgruppen, „Energie Norm“ mit 11,6 und „Energie Hoch“ mit 12,4 Megajoule umsetzbare Energie pro Kilogramm Trockenmasse, eingeteilt. Die unterschiedlichen Energiegehalte im Futter wurden durch Abstufungen der Gehalte an Kraftfutter und Maissilage in den Rationen erreicht. Während des Versuches wurden die Tiere fünf Schlachtgruppen mit 120, 200, 400, 600 und 780 Kilogramm Mastendgewicht zugeordnet. Im Rahmen der Schlachtung und der darauffolgenden Schlachtkörperzerlegung wurden die Körper der Tiere in einzelne Gewebefraktionen zerlegt. Diese wurden anschließend homogenisiert und hinsichtlich ihrer Nährstoffzusammensetzung analysiert. Anschließend wurden Regressionsgleichungen für die Körperzusammensetzung der Bullen im Wachstumsverlauf erstellt. Aus der ersten Ableitung der einzelnen Gleichungen wurde die Zusammensetzung des Zuwachses und die Veränderung der Körperproportionen im Wachstumsverlauf berechnet.

Die Ergebnisse dieses Forschungsprojektes wurden in zwei Publikationen veröffentlicht. Ziel der ersten Publikation war es, die Mast- und Schlachtleistung von Fleckviehbullen der heutigen Generation bei definierten Endgewichten und unter dem Einfluss der Fütterung mit unterschiedlichen Energiegehalten darzustellen. Die Ergebnisse haben gezeigt, dass Fleckviehbullen der aktuellen Genetik höhere Zuwachsleistungen und Endgewichte erreichen als Fleckviehbullen in früheren Studien. Heutige Fleckviehbullen konnten die im Futter angebotenen Energie- und Nährstoffgehalte sehr effizient verwerten, was sich in hohen täglichen Zunahmen bis hin zu hohen Endgewichten widerspiegelte. Die mit erhöhter Energiekonzentration gefütterten Bullen zeigten im Vergleich zu Bullen der Energie Norm Gruppe eine höhere Zuwachsleistung. Unterschiede in der Schlachtkörperzusammensetzung und Fleischqualität von Bullen beider Fütterungsgruppen konnten nicht festgestellt werden. Folglich benötigten die mit normaler Energiekonzentration gefütterten Bullen mehr Zeit bis zum Erreichen des höchsten angestrebten Endgewichtes. Die Schlachtleistung und Fleischqualität der Bullen der Energie Norm Gruppe war jedoch in allen Gewichtsgruppen vergleichbar mit der von hochenergetisch gefütterten Bullen.

Ziel der zweiten Veröffentlichung war die Bestimmung der Gewebe- und Nährstoffzusammensetzung sowie der Zusammensetzung des Zuwachses von wachsenden Fleckviehbullen nach Fütterung mit unterschiedlichen Energiegehalten. Anhand der Ergebnisse wurde deutlich, dass die Fütterung mit unterschiedlichen Energiegehalten keinen Einfluss auf die Körperzusammensetzung und den Energie- und Nährstoffansatz wachsender Fleckviehbullen hatte. Im Wachstumsverlauf der Fleckviehbullen zeigten sich ungleichmäßige Veränderungen im Gewebezuwachs und Nährstoffansatz, welche auf allometrisches Wachstum der Tiere hindeuten. Der Vergleich mit früheren Studien zeigte, dass heutige Fleckviehbullen, insbesondere in hohen Gewichtsgruppen, einen geringeren Ansatz an Rohprotein, jedoch einen höheren Ansatz an Rohfett und Energie aufweisen. Daher sollten die Empfehlungen zur Energie- und Nährstoffversorgung von wachsenden Fleckviehbullen regelmäßig an die aktuellen Energie- und Nährstoffbedürfnisse sowie an die steigenden Mastendgewichte und Tageszunahmen der Tiere angepasst werden.

Zusammenfassend zeigten sich bei wachsenden Fleckviehbullen der Fütterungsgruppen Energie Norm und Energie Hoch keine Unterschiede in der Körperzusammensetzung, Schlachtkörperzusammensetzung, Zusammensetzung des Zuwachses und den Fleischqualitätsmerkmalen. Daraus lässt sich schlussfolgern, dass eine Fütterung der Tiere mit erhöhter Energiekonzentrationen aus metabolischer Sicht nicht notwendig ist. Fleckviehbullen können entsprechend ihrer Physiologie wiederkäuergerecht mit niedrigeren Energiegehalten und damit grobfutterreichen Rationen gefüttert werden, wodurch ein positiver Einfluss auf das Tierwohl entsteht. Zukünftige Fütterungskonzepte sollten den Grobfutteranteil in den Rationen für Rinder erhöhen, um so die Konkurrenz um Ressourcen für die Produktion von Nahrungsmitteln und Futtermitteln zu reduzieren. Außerdem sollten Phasenfütterungskonzepte angewendet werden, um wachsende Rinder entsprechend ihres Energie- und Nährstoffbedarfes zu füttern und so Stickstoffausscheidungen und damit verbundene Umweltbelastungen zu reduzieren. Auf diese Weise können nachhaltigere Fütterungskonzepte zur Schonung natürlicher Ressourcen, zum Umweltschutz und zu mehr Tierwohl beitragen.

1 General introduction

In agriculture, farm animals are primarily kept for the production of animal products such as milk, eggs, or meat. To ensure the animals' performance, livestock feeding conditions must be adapted to the needs of the farm animals. Hence, animal nutrition is specifically tailored to the species, breed, sex, stage of maturity, performance level, and production goals of the respective livestock. For this purpose, various feeding concepts are available, which serve the farmer as guidelines for appropriate animal feeding.

Feeding recommendations comprise information on energy and nutrient requirements based on a particular animal's live weight and daily gain. Such recommendations provide a useful tool for livestock farmers to ensure a feed composition that meets the animals' requirements to optimize growth and ensure productivity and health. To determine the appropriate recommendations, it is necessary to know the animal's nutrient and energy requirements for maintenance and performance. Hence, how much energy and nutrients are needed to maintain the body's physiological processes and how much are stored in the body at a specific live weight.

This thesis aims to evaluate feeding concepts for growing cattle. Therefore, it is necessary to determine the amount of energy and nutrients cattle need for physiological growth processes. These requirements depend on body composition and composition of body weight gain, which in turn depend on the respective cattle breed and sex and change in the course of animal growth.

1.1 Feeding strategies for growing cattle

This thesis considers growing Fleckvieh beef bulls at the current genetic level. The Fleckvieh breed, also known as German Simmental, is a dual-purpose cattle breed that simultaneously provides high milk and meat yields. The performance potential of Fleckvieh cattle has been improved by selective breeding during the past decades (Honig et al., 2020, 2022). Fleckvieh cows were bred for higher milk yield, leading to increased frame sizes (Krogmeier, 2009). Furthermore, breeding Fleckvieh cattle for beef traits such as fattening, and slaughter performance is an integral part of the breeding program (Kalcher, 2015). Consequently, current Fleckvieh bulls feature increased daily weight gains (Honig et al., 2020), which may have an effect on the animals’ energy and nutrient requirements. The amount of energy and nutrients that cattle need for body weight gain during the growth process changes due to the development of individual body tissues. Since body weight gain has increased in past decades, it can be expected that current Fleckvieh bulls may be less resilient to variations in feed energy concentrations and are dependent on an optimal feed energy supply.

Research into body composition and the composition of body weight gain in Fleckvieh bulls was performed about 30 years ago (Augustini et al., 1992; Kirchgessner, et al., 1993; Kirchgessner et al., 1994; Otto et al., 1994). A component of these investigations was determining the energy and nutrient accretion in growing Fleckvieh bulls within a 200–650 kg live-weight range (Schwarz et al., 1995a). Based on the results, recommendations for the energy and nutrient requirements of German Fleckvieh beef cattle were calculated and published by the Society of Nutrition Physiology (GfE) in 1995. Feeding recommendations for Fleckvieh beef bulls cover a live-weight range from 175–625 kg and daily weight gains from 800–1600 g at specific growth stages (GfE, 1995). The energy and nutrient accretion rates specified in these feeding recommendations are shown in Table 1.1 and indicate increasing crude protein, crude fat, and energy accretion rates in growing bulls (GfE, 1995).

The current situation in cattle fattening farms shows that farming conditions have changed in the past decades. Continual selective breeding and progress in cattle farming and feeding improved the growth potential of Fleckvieh bulls. This practice is reflected in increased animal daily weight gains and final weights (Honig et al., 2020). The increased fattening performance in current Fleckvieh bulls exceeds the scope of application provided in the GfE (1995) feeding recommendations. At present, the feeding recommendations for

Table 1.1: Daily accretion rates of crude fat, crude protein, and energy in Fleckvieh bulls with different live-weight ranges and daily weight gains
(adapted from GfE, 1995).

	200–350 kg live weight					
Daily weight gain (g)	1000	1100	1200	1300	1400	1500
Fat accretion (g)	164	180	196	213	229	245
Protein accretion (g)	175	193	210	228	245	263
Energy accretion (MJ)	10.3	11.4	12.4	13.5	14.5	15.5
	350–500 kg live weight					
Daily weight gain (g)	800	900	1000	1100	1200	1300
Fat accretion (g)	141	158	176	193	211	229
Protein accretion (g)	140	156	175	192	210	228
Energy accretion (MJ)	8.6	9.7	10.8	11.9	13.0	14.1
	500–650 kg live weight					
Daily weight gain (g)	700	800	900	1000	1100	
Fat accretion (g)	144	165	186	207	227	
Protein accretion (g)	144	165	185	206	227	
Energy accretion (MJ)	9.1	10.2	11.5	12.7	14.0	

German Fleckvieh cattle are calculated by the Bavarian State Research Center for Agriculture (LfL), based on GfE recommendations and the results of current feeding experiments (LfL, 2020). The LfL feeding recommendations are continuously adapted to the fattening performance and target weights of current Fleckvieh bulls. However, intensive fattening could have changed the bulls' body composition in terms of body tissue and nutrient composition. This change could affect the energy and nutrient requirements of Fleckvieh bulls and increase sensitivity to variations in feed energy concentrations.

The ability to respond to varying nutrient and energy levels in the feed and thus maintain normal growth processes under changing nutritional conditions is essential because regional differences in arable farming conditions can influence forage production and quality. Furthermore, climate change is expected to influence feed production. In recent years, farmers have had to deal with adverse weather conditions, such as severe heat waves, which are expected to last longer and appear more frequently in the future (Meehl

& Tebaldi, 2004). Progressive climate change is associated with an increased frequency of heat weaves and droughts (Schär et al., 2004; Li et al., 2009), which can result in reduced crop yields (Trnka et al., 2004; Li et al., 2009) and decreased forage quality (Lee et al., 2017). Conversely, climate change is also expected to induce heavy rainfall during the summertime in large parts of Europe (Christensen & Christensen, 2003). Rosenzweig et al. (2002) demonstrated that frequent extreme precipitation events under changing climate conditions could reduce maize yields due to excess soil moisture.

Variation in forage quality and quantity can affect cattle growth in various ways. Research into the shortage of energy and nutrient supply under restricted feeding conditions showed lower daily weight gains, extended fattening periods, decreased muscle and fat accretion, and decreased carcass fat class scores in insufficiently fed cattle (Keogh et al., 2015; Manni et al., 2017). Moreover, Inhuber et al. (2021) demonstrated that reducing dietary crude protein in rations with equal energy content led to an effect similar to that of feed restriction, resulting in inferior fattening and slaughter performance of cattle fed low protein rations.

Extended fattening periods and inferior carcass traits in malnourished cattle cause economic losses for cattle farmers, which could be avoided by providing a diet that meets the animals' demands. Moreover, a needs-based protein supply ensures animal health by maintaining a functioning immune system (Li et al., 2007) and preventing cattle lameness (Manson & Leaver, 1988). In addition, research by Todd et al. (2006) and Xia et al. (2018) revealed that lower crude protein proportions in cattle diets reduced nitrogen excretion and ammonia emissions. Hence, adequate feeding recommendations that reflect the nutrient and energy demands of beef cattle ensure good fattening performance and minimize the negative environmental impacts of cattle farming.

Conventional cattle feeding strategies aim to increase the production of animal products within a specific time frame by using high-quality feedstuffs, such as wheat, soya beans, and maize, as concentrates for cattle feeding. This strategy should be critically evaluated because feed production competes with human food production for resources such as land, water, and energy. In particular, cultivating crops for use as concentrates competes directly with human nutrition. Competition can be reduced by feeding cattle with forage that is unsuitable for humans, such as intermediate crops from crop rotation, non-edible crop products from food-supplying plants (e.g., straw), or grass pasture. Hence, future feeding concepts should aim to reduce food competition by feeding cattle with roughage-rich rations according to their physiological advantages as ruminants. (Flachowsky et al., 2017; Windisch & Flachowsky, 2020)

1.2 Cattle growth patterns and maturity types

Feeding concepts for growing cattle must be geared to the nutritional requirements of the animals. Cattle growth comprises body weight gain and phenotypic changes. Owens et al. (1993) stated that growth and development differ from each other. While growth is related to increased body weight and tissue gain, development refers to the maturation of individual tissues and body parts (Owens et al., 1993).

Individual body fractions grow and develop at different rates during various stages of the animal's maturity (Hammond, 1950; Berg & Butterfield, 1968; Owens et al., 1993), a process commonly known as ontogenetic allometry or allometric growth. For many years, scientists have attempted to explain animal growth using mathematical functions. Snell (1892) was the first to create a function to describe animal brain weight in relation to body weight. Huxley (1924; 1932) later used Snell's function to describe allometric growth in animals as $y = bx^k$, where y expresses the size or weight of a body fraction, x represents the size or live weight of the animal, and b and k are constants.

Huxley (1932) stated that the constant k represented the growth coefficient of a body part and could be used as an indicator of its development. When the body part grows at the same pace as the body, a condition called isogony, $k = 1$, and no changes in the body part size in relation to the body are expected. Heterogony occurs when a body portion grows at a different rate to the body and is an allometric condition. The latter state can be differentiated using negative heterogony (also known as negative allometry) as $k < 1$ when a body part grows slower than the body. Conversely, in positive heterogony (positive allometry), $k > 1$ when a body part grows faster than the body. Using the constant k, the power function $y = bx^k$ describes allometric growth in animals. (Huxley, 1932)

Body tissue growth begins at the point of conception and proceeds until the animal has reached maturity. Previous studies have classed individual body tissues into early, intermediate, and late-growing tissues (Hammond, 1950; Berg & Butterfield, 1968; Owens et al., 1993). Body tissues reach their peak growth rates at different times, depending on the animal's age, as illustrated in Figure 1.1. Early growing body tissues such as bone tissue reach their peak growth rates first, followed by intermediate-growing muscle tissue and late-growing fat tissue (Hammond, 1950; Berg & Butterfield, 1968; Owens et al., 1993). This growth sequence can be explained by the demands on growing animals' bodies. Bone tissue grows at an early stage of life, as a functioning skeletal system is essential for a newborn calf. Muscles reach their peak growth rate with increasing movement in young

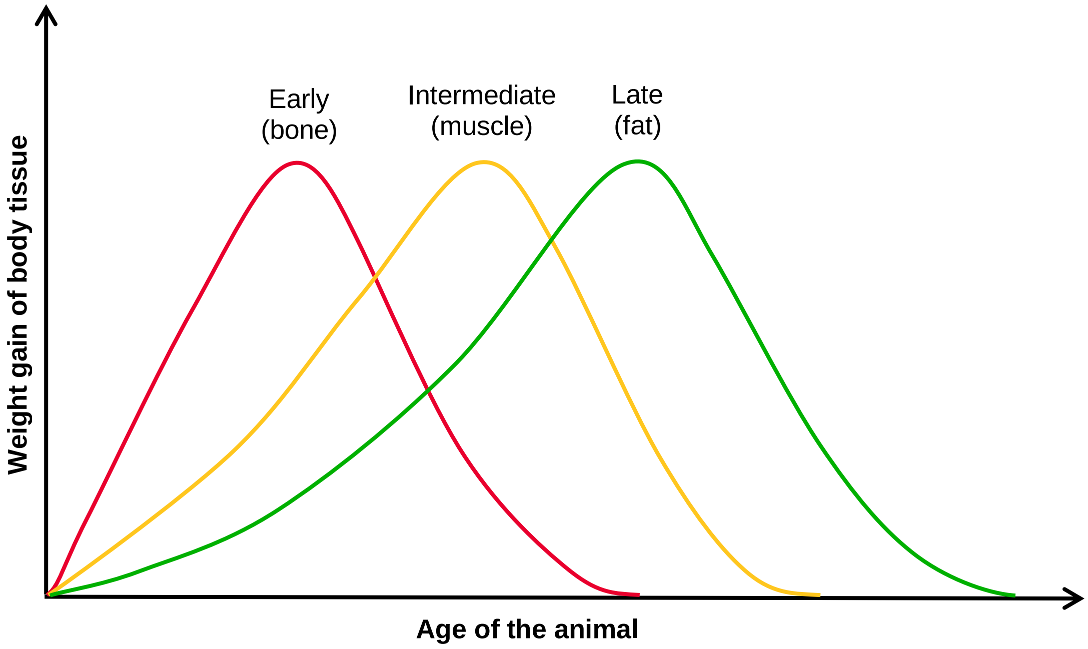

Figure 1.1: Growth sequence of early, intermediate and late growing body tissues (adapted from Hammond, 1950).

animals. The proportion of fat tissue increases especially in the late stage of maturity when extensive amounts of crude fat are stored in fat cells to provide energy reserves for times of shortage.

Furthermore, Owens et al. (1993) stated that tissue development could be early, intermediate, or late, depending on the tissue's location in the animal's body. Hence, fat tissue can be described as late growing, yet within fat tissue, suet shows early development. Intermuscular and subcutaneous fat tissues show intermediate growth, and intramuscular fat tissue shows late development. (Owens et al., 1993)

Developmental processes in individual body tissues involve changes in the tissue's chemical composition and, consequently, changes in the body's chemical composition. Therefore, animal growth processes can be studied by examining gains in body tissues and their chemical components during different stages of maturity until the animal has reached an adult stage.

According to Owens et al. (1993), maturity is attained when the amount of muscle tissue in the animal's body reaches a maximum. Owens et al. (1995) later elaborated on this observation by stating that maturity is reached when protein gain stops. Mature animals should have a constant body composition when fed according to their maintenance requirements. However, cattle kept for beef production are not usually fattened until they reach maturity. Nonetheless, cattle farmers select animals for slaughter at a particular stage of maturity when the animals yield high-grade carcasses. The time chosen for slaughter depends on the cattle breed and the cattle maturity type.

Cattle breeds can be classified into several maturity types that differ according to their growth and development rates. Basically, two types can be distinguished: early-maturing and late-maturing cattle breeds. Early-maturing cattle breeds, such as Angus and Hereford, differ from late-maturing breeds, such as Charolais and Fleckvieh, by exhibiting smaller frame sizes and faster physiological growth processes. Faster growth and development processes in early-maturing cattle breeds result in lower final weights and slaughter ages. Lower final weights depend on higher fat accretion rates in early-maturing breeds, which induces higher intramuscular fat content and carcasses with higher fat proportions but lower muscle proportion (Keane, 2011). According to Berg and Butterfield (1976), early-maturing cattle breeds can be fattened using restricted energy and nutrient supply and meet the needs of meat markets, which target lower carcass weights and higher intramuscular fat content.

Conversely, late-maturing cattle breeds are characterized by higher growth potential, higher daily weight gains, and increased feeding and energy efficiency than early-maturing breeds (Geay & Robelin, 1979). Furthermore, late-maturing cattle have the advantage of slow fat accretion and thus can be fattened to achieve higher final weights (Berg & Butterfield, 1976). This observation was confirmed by Augustini et al. (1992) and Kirchgessner et al. (1994), who demonstrated that late-maturing Fleckvieh cattle exhibited high rates of protein gain. Geay and Robelin (1979) concluded that feeding intensity should be geared to cattle maturity types. Feeding recommendations that adequately reflect the amounts of energy and nutrients needed for physiological growth processes can help to exploit the performance potential of different cattle breeds.

1.3 Thesis objectives

The objective of this thesis is to generate basic data for determining the nutrient and energy requirements of growing Fleckvieh beef bulls under different feeding conditions. For this purpose, analyses of body composition and nutrient and energy accretion rates in Fleckvieh bulls fed rations with varying energy concentrations were performed and previously described by Honig et al. (2020; 2022; Chapters 3 & 4). The results were used to illustrate patterns of allometric growth in cattle and to show how the sustainability of cattle feeding concepts can be improved.

Basic research on body composition and energy and nutrient accretion in growing Fleckvieh bulls was performed about 30 years ago (Augustini et al., 1992; Kirchgessner et al., 1993; Kirchgessner et al., 1994; Otto et al., 1994). In past decades, continual selective breeding and progress in cattle farming and feeding improved the growth potential of Fleckvieh bulls. This practice is reflected in increased daily weight gains and final animal weights. Furthermore, intensive fattening could change animal body composition in terms of body tissue and nutrients, influencing the energy and nutrient requirements of growing Fleckvieh bulls and leading to a low resilience to variations in feed energy concentrations. Therefore, this thesis investigates how growth patterns in Fleckvieh bulls change under the influence of varying feed energy concentrations and how typical allometric growth proceeds in cattle.

For this study (Chapters 3 & 4), Fleckvieh bull calves were customarily reared and, for the fattening period, allocated to normal energy (NE) and high-energy (HE) treatment groups fed 11.6 and 12.4 MJ metabolizable energy (ME) per kg dry matter (DM), respectively. Differences in feed energy concentrations were achieved by varying the amount of concentrate in the rations. For the NE treatment, the feed energy volume reflected current practical conditions based on the recommended energy supply for fattening Fleckvieh bulls (LfL, 2020). The high amount of metabolizable energy in the HE rations was achieved by feeding concentrate amounts that far exceeded the quantities typically used in Germany. Hence, an energetic differentiation of 0.8 MJ ME/kg DM between the two diets was achieved. Investigating how current Fleckvieh bulls cope with an extraordinarily HE supply should provide a better understanding of the breed’s physiological capabilities. Feeding bulls HE rations is expected to produce higher body fat content and accretion rates, especially in animals with high live weights.

A serial slaughter trial was conducted to observe the effects of HE feeding and growth on the body composition, composition of gain, and allometric growth processes in Fleckvieh bulls. Serial slaughter refers to slaughter at defined growth stages. Such trials can be performed with animals of the same age or a similar stage of maturity. This project aims to describe nutritional influences on processes of allometric growth in cattle. Therefore, slaughter was performed at defined final weights and thus specific stages of maturity. Bulls from both feeding groups were slaughtered at final live weights of 120, 200, 400, 600, and 780 kg. During slaughter and subsequent beef cutting, the bulls' bodies were dissected to individual body tissue fractions, which were weighed, sampled, homogenized, and analyzed for their chemical composition. Next, the chemical composition of the bodies of growing Fleckvieh bulls was determined from the chemical composition of the individual body tissues. Data on the body composition of growing bulls was used to calculate the gain composition and thus illustrate allometric growth patterns in cattle.

The analysis of cattle growth processes under different feed energy concentrations was an essential part of this project. Data on growth performance, feed, energy, and nutrient intake, and nutrient and energy accretion in growing Fleckvieh bulls were provided. Consequently, the project allowed an evaluation of feeding recommendations for Fleckvieh bulls. The results were used to consider feeding strategies that could contribute to more sustainable cattle feeding in the future.

1.4 Thesis outline

This doctoral thesis aims to generate basic data for determining the nutrient and energy requirements of Fleckvieh bulls. Hence, analyses of body composition, gain composition, and processes of allometric growth in Fleckvieh beef bulls under varying feeding conditions were performed. The materials and methods employed in this study are described in Chapter 2, which contains information about the feeding experiment's implementation and serial slaughter trial (Chapter 2.1) and slaughter and tissue sampling methods (Chapter 2.2). Furthermore, the analysis of feedstuffs, body tissues, and meat quality traits are described (Chapter 2.3), and an overview of the data analysis is provided (Chapter 2.4).

The results of this study are presented in two publications. The first publication (Honig et al., 2020; Chapter 3) specifies the fattening and slaughter performance of current Fleckvieh bulls at defined final weights and under the influence of varied feed energy concentrations. The study comprises results on feed, energy, and nutrient intake, and the average daily weight gain of growing bulls. Furthermore, the dressing percentage and carcass tissue composition, such as muscle, tendon, bone, and fat tissue, of bulls in different final weight groups are presented. The proportions and tissue composition of carcass quarters and individual beef cuts are also specified. The investigation was completed by determining the rib-eye area and meat quality traits of Fleckvieh bulls with different final weights. Carcass composition and meat quality traits were compared between late-maturing Fleckvieh bulls and early-maturing beef cattle breeds to demonstrate the advantages of meat production in late-maturing dual-purpose Fleckvieh bulls.

The second publication (Honig et al., 2022; Chapter 4) analyzes the body tissue composition and chemical composition of growing Fleckvieh bulls fed rations of varying energy concentrations. In this context, the gain composition is considered. Moreover, the feed and energy efficiency of growing bulls fed regular and HE diets is indicated. The body composition data for growing bulls comprises the proportions of body tissue fractions, such as hide, blood, organs, gastrointestinal tract, fat, muscle, tendon, and bone. Individual body tissues were analyzed for their chemical composition, including water, crude ash, crude protein, crude fat, and energy content. The body composition data was used to calculate the accretion rates of individual body tissues, chemical components, and energy in growing Fleckvieh bulls within a live-weight range of 100–800 kg. The energy and nutrient accretion rates in growing bulls were used to evaluate feeding recommendations for Fleckvieh beef cattle.

A comprehensive discussion of the results is divided into several chapters. First, the effects of feeding varying amounts of energy on the fattening performance, body composition, and carcass traits of Fleckvieh bulls are discussed (Chapter 5). The discussion expands on modeling the gain composition and thus illustrating processes of ontogenetic allometry in cattle (Chapter 5.1). The results are used to specify daily accretion rates of crude protein, crude fat, and energy in Fleckvieh bulls at different live weights and daily weight gains and thus evaluate recommendations for the energy and nutrient requirements of the animals. Subsequently, allometric growth patterns in body tissues and nutrients are discussed (Chapter 5.2). Finally, it is demonstrated that more sustainable cattle feeding concepts could contribute to increased resource efficiency, environmental protection, and animal welfare (Chapter 5.3).

The discussion is followed by the research conclusions and outlook (Chapter 6). This chapter provides an overview of the most significant results of this thesis and highlights the research required to improve the sustainability of feeding concepts for growing cattle.

2 General methodology

The materials and methods described in this section expand on the experimental design described by Honig et al. (2020; 2022; Chapters 3 & 4).

This research project aims to generate basic data for determining the nutrient and energy requirements of growing Fleckvieh beef bulls under different feeding conditions. To determine appropriate feeding recommendations for cattle, it is necessary to know the amount of energy and nutrients the animal requires for maintenance and performance. That is, how much energy and nutrients are needed to maintain the body's physiological processes and how much are stored in the body at a specific live weight.

To detect the amounts of energy and nutrients required by cattle, feeding experiments were conducted, in which animal performance was observed under different feeding conditions. Adequately calculating the feeding recommendations for growing cattle requires knowledge about the energy and nutrient accretion of the animals at different growth stages. Therefore, it is necessary to conduct a serial slaughter trial to determine the body composition and rates of energy and nutrient gain at different stages of maturity. The same research approach can be used to describe processes of allometric growth in cattle and the influence of dietary energy concentration on cattle growth. The only way to describe ontogenetic allometry in cattle and the influence of nutrition on cattle growth is to analyze the body composition of cattle at defined stages of maturity. Therefore, it is preferable to address both research questions simultaneously to gain more knowledge from fewer animal experiments.

An overview of the experimental procedures conducted in this study is illustrated in Figure 2.1. Bulls were slaughtered at defined stages of maturity, and the bulls' bodies were dissected into different body tissue fractions. A chemical analysis of the individual body tissue fractions was conducted to calculate the empty body's chemical composition. Next, the tissue, nutrient, and energy gain per kg of empty body weight gain was calculated. The results provided an evaluation of the feeding recommendations for Fleckvieh bulls and a precise representation of allometric growth processes in cattle.

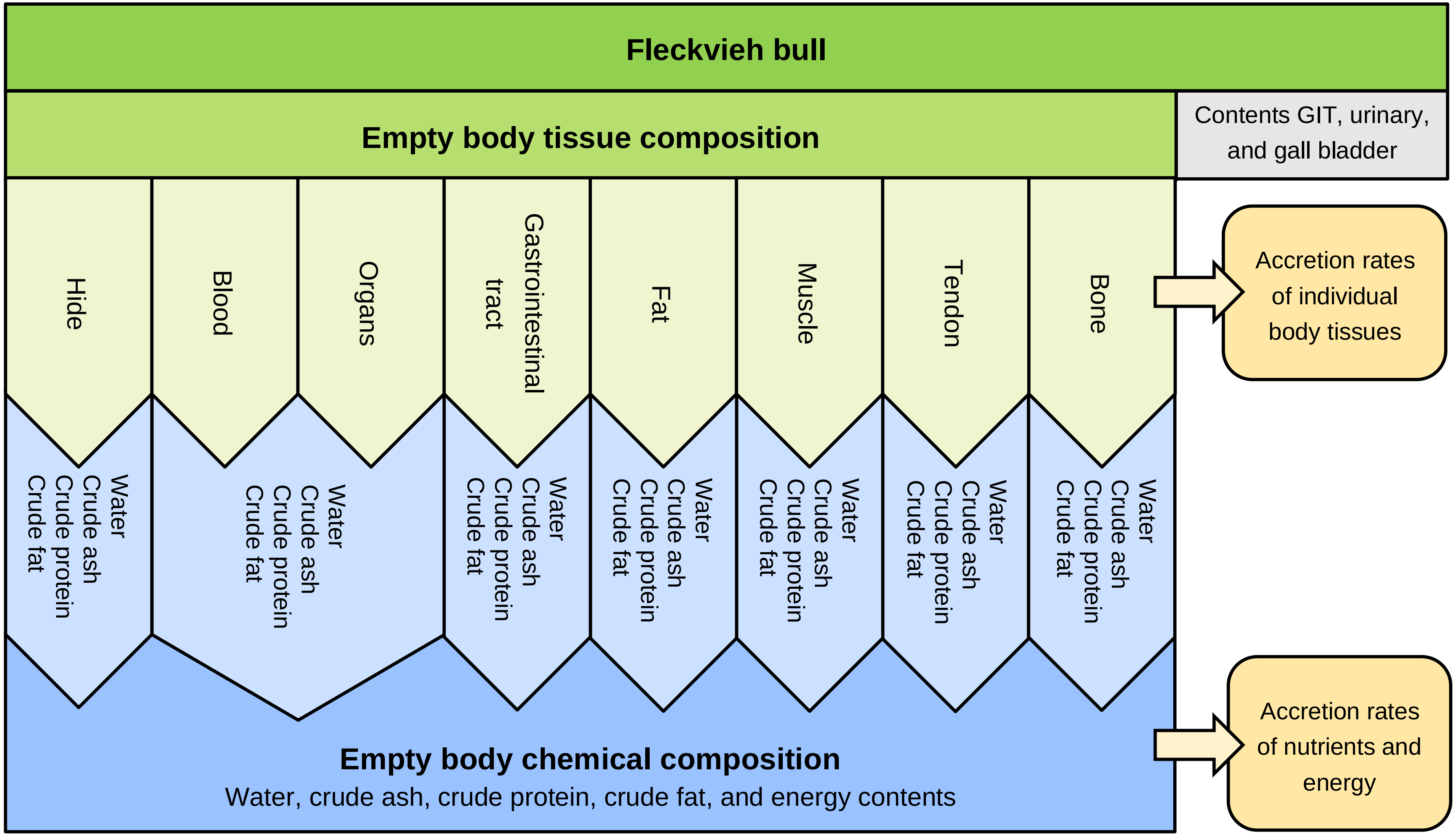

Figure 2.1: Analysis of empty body tissue and chemical composition, and body tissue, nutrient, and energy accretion rates.

2.1 Feeding experiment and serial slaughter trial

The experimental design comprised a feeding experiment ending with a serial slaughter trial and was previously described by Honig et al. (2020; 2022; Chapters 3 & 4).

The research was conducted at the Bavarian State Research Center for Agriculture (LfL) according to European guidelines for animal experiments (Directive 2010/63/EU, 2010) and approved by the ethics committee of the LfL Ethics of Animal Experiments. The trial included 72 Fleckvieh bull calves from cattle farms in Bavaria, Southern Germany. The calves entered the trial aged 42 d ±9, had a body weight (BW) of 80 kg ±6 and were customarily reared as described in Chapter 3.2.1.

The fattening period was initiated at an average BW of 225 kg ±29 and age of 154 d ±15. Bulls were fed two different total mixed rations (TMRs) based on maize silage and concentrates for *ad libitum* intake. The TMRs showed significant differences in the amount of metabolizable energy, which allowed the effect of dietary energy concentration on growth performance and body development processes to be investigated. Bulls were allocated to the NE and HE treatment groups with 11.6 and 12.4 MJ ME/kg DM, respectively. The differences in TMRs' energy concentrations were achieved by varying the percentages of maize silage and concentrates. Bulls in the NE group were fed rations with 80% maize silage and 20% concentrates, while animals in the HE group were fed rations with 40% maize silage and 60% concentrates (basis DM). Crude protein content per kg DM remained constant in both diets.

For the serial slaughter trial, five weight groups were chosen to represent cattle growth at different stages of maturity in a conventional fattening system. The weight groups were selected during sensitive stages of calf rearing and fattening. In the first weight group, eight animals with 120 kg live weight were slaughtered just before weaning. Thus, the physiological body condition of the gastrointestinal tract under the influence of milk replacer feeding and before the complete adjustment to roughage digestion could be recorded. The number of animals in the lowest weight group was less than in the other weight groups because little variation in body composition was expected at low live weights. In the second weight group, 10 animals with 200 kg live weight were selected just before initiating the fattening period to provide basic data on body composition before the feed energy differentiation through NE and HE treatment.

To represent different stages of the fattening period within the serial slaughter trial, bulls of both energy treatment groups were slaughtered at the beginning (400 kg, 9+9 animals), the midterm (600 kg, 9+9 animals), and the end of the fattening period (780 kg, 9+9 animals). In summary, the serial slaughter trial included animals with a live-weight range of 120–780 kg weight and a feeding regime with two different energy levels, as illustrated in Figure 2.2. Differences in the slaughter age of bulls in the same weight group had to be accepted since the animals were slaughtered at defined final weights.

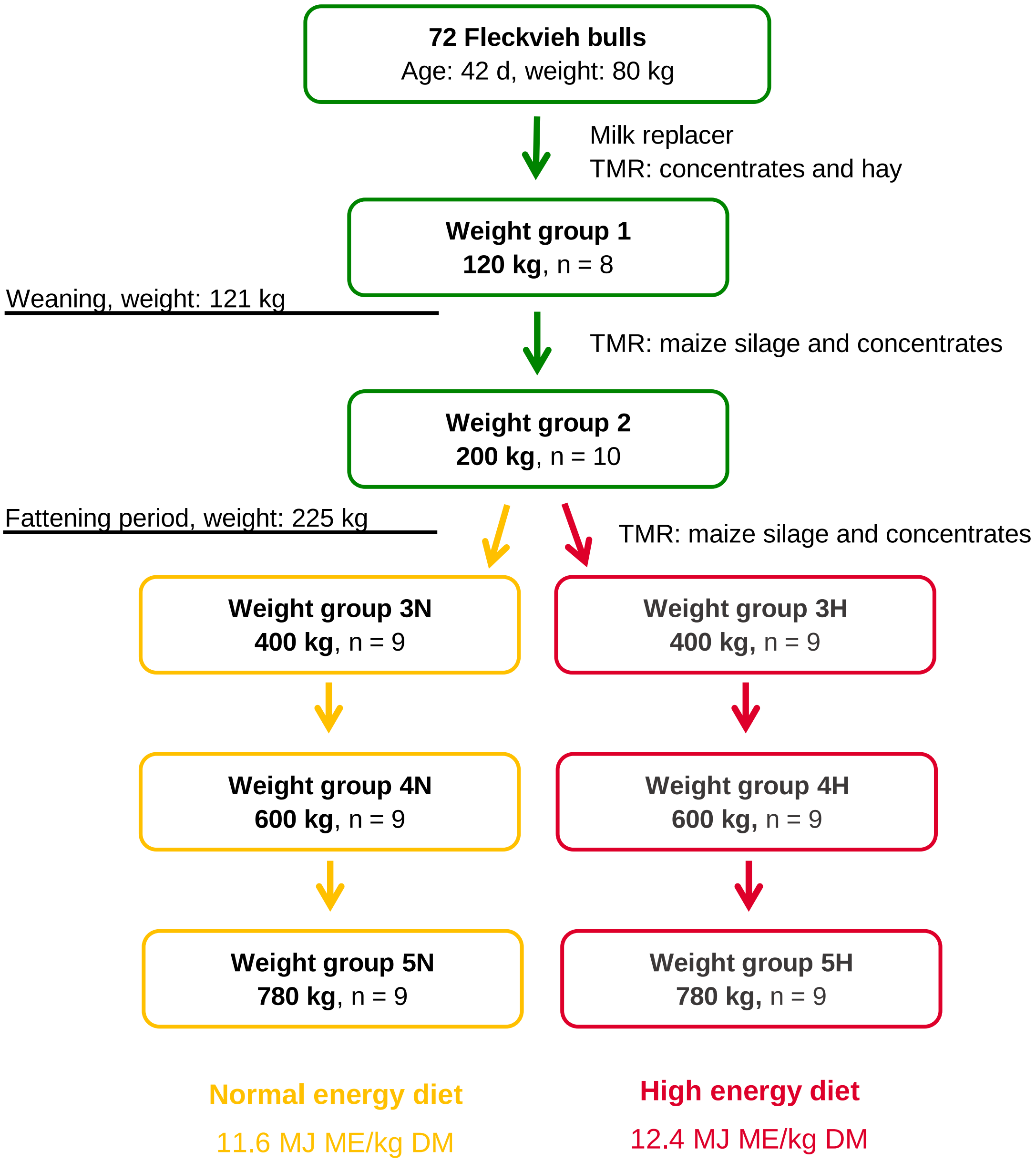

Figure 2.2: Weight groups and feeding groups.

2.2 Slaughter and tissue sampling

This chapter expands on slaughter and tissue sampling methods previously described by Honig et al. (2020; 2022; Chapters 3 & 4). Slaughter and meat cutting took place at the Research Abattoir in Grub, Germany, and was carried out in compliance with Council Regulation (EC) No 1099/2009 (2009).

The bulls' final live weights were determined after stunning with a cattle gun and before bleeding. During slaughter, the bulls' empty body weights (EBW) were determined as the final live weight minus the contents of the gallbladder, urinary bladder, and gastrointestinal tract (GIT). The entire empty body was dissected into body tissue fractions: hide, blood, organs, empty GIT, body fat, muscle, tendon, and bone. The composition of the individual body tissue fractions is shown in Table 2.1.

Table 2.1: Components of body tissue fractions.

Tissue fractions	**Components**
Hide	Hide from the right side of the body
Blood	Blood collected during bleeding
Organs	Brain, eyes, tongue, spinal cord, thymus, heart, lung, diaphragm, liver with gall bladder, spleen, pancreas, kidneys, urinary bladder, penis, testicles
Gastrointestinal tract	Esophagus, rumen, reticulum, omasum, abomasum, small intestine, large intestine
Fat	Visceral fat: suet, pelvic fat, organ fat trims, greater omentum, lesser omentum, mesentery, scrotum fat Carcass fat: subcutaneous fat and intermuscular fat from the right side of the carcass
Muscle	Muscles from the right side of the carcass
Tendon	Tendons from the right side of the carcass
Bone	Bones from the right side of the skull and carcass, bones from the right feet, tail bones

The blood was quantitatively collected during bleeding and weighed afterward. The front and rear feet were manually removed between the carpus and metacarpus and the tarsus and metatarsus and weighed separately. Hooves were removed using a hydraulic hock cutter and weighed. The front and rear feet of the right side of the body were dissected to hide, tendon and bone tissues, and each tissue was weighed individually. Dehiding, evisceration, carcass halving, and trimming were carried out according to European standards (Commission Regulation (EC) No 1249/2008, 2008). Dehiding was performed manually, taking great care to separate the hide from subcutaneous fat tissue, which remained with the carcass. After dehiding, the entire body hide was weighed and divided along the dorsal line. The right half of the hide was cut into pieces and stored at -18 °C for further processing. The head of the skinned animal was removed, weighed, and dissected to organs (brain, eyes, tongue), muscle, and bone tissues. During evisceration, the organs were collected, fat trimmed, and weighed without fat trimmings. Fat tissue was manually removed from the GIT. Afterward, the GIT, including its contents, was weighed, emptied, washed, hung up to drain, and weighed again as an empty GIT.

After cooling for 20 hours at 4 °C, the right side of the carcass was dissected. The carcass was quartered between the eighth and ninth ribs and cut into commercial beef cuts using cutting methods of the German Agricultural Society (DLG, 1985). Each cut was manually dissected to muscle, tendon, fat, and bone tissue. The cuts, and their tissues, were weighed separately. The bones from the right side of the body were stored at -18 °C for further processing. The organs, combined with the blood, were ground using a meat grinder and sampled in one batch. Similarly, body fat, muscle, tendon, and GIT tissue fractions were ground separately in a meat grinder. The meat grinder was disassembled and cleaned after each tissue batch. Individual tissue samples were taken, and all samples were stored at -18 °C. The hide portions were later homogenized using a bowl cutter and frozen bones were crushed using a bone crusher. After processing, the hide and bone tissues were sampled individually, and the samples were stored at -18 °C. This procedure allowed body tissue samples to be collected and stored for chemical analysis at a later date.

2.3 Analysis of feedstuffs, meat quality traits, and body tissues

The chemical and physical analysis of feedstuffs, body tissues, and meat quality traits was conducted at the LfL Department of Quality Assurance and Analytics. The analysis procedures were previously described by Honig et al. (2020; 2022; Chapters 3 & 4).

Chemical analysis of the individual feedstuffs given during calf rearing and the fattening period is described in Chapter 3.2.3. Feed components were sampled and analyzed individually. The feed components were analyzed for the contents of dry matter, crude ash, crude protein, crude fat, sugar, starch, and neutral detergent fiber with amylase solution and without residual ash. Furthermore, the metabolizable energy content of the feedstuffs was calculated from the individual analyses. The analyses were performed to determine the energy and nutrient content of the feedstuffs and thus calculate the animal's individual daily energy and nutrient intake.

Meat quality traits of growing Fleckvieh bulls were analyzed using a sample of the longissimus thoracis muscle (9th and 10th rib cuts), as described in Chapter 3.2.5. The rib-eye area of the 9th rib was measured using digital image analysis. Muscle pH was measured on three separate occasions after slaughter. Furthermore, intramuscular fat content, meat color, aging loss, cooking loss, and shear force were measured to complete the analysis of the meat quality traits. Results were used to evaluate the influence of growth and energy consumption on the rib-eye area and meat quality traits and provide recommendations on fattening concepts and target weights in Fleckvieh bulls.

Chemical analysis of the Fleckvieh bulls' body tissues is described in Chapter 4.2.3. The chemical composition of individual body tissues was analyzed to determine the chemical tissue composition concerning crude fat, crude protein, crude ash, and water content. The energy content of each tissue was calculated according to Böhme and Gädeken (1980), which determined the energy content of crude fat and crude protein in cattle to be 39.0 kJ/g and 22.6 kJ/g, respectively. The tissue weights, energy contents and chemical tissue compositions were used to calculate the energy content and chemical composition of the bulls' empty bodies. Results of body tissue composition and body chemical composition were used to calculate the gain composition of body tissues and nutrients in growing Fleckvieh bulls.

2.4 Data analysis

Data analysis was performed to statistically confirm the results and correctly identify differences between animal weight groups and feeding groups. This section briefly describes the principal data analysis and modeling methods. Detailed descriptions can be found in the publications (Honig et al., 2020, 2022; Chapters 3 & 4).

In Chapter 3, statistical analysis of daily feed, energy, and nutrient intake, fattening and slaughter performance, carcass tissue composition, beef cut tissue composition and meat quality traits in growing Fleckvieh bulls fed rations with varying energy concentrations was performed. Hence, the effect of HE feed intake on fattening and slaughter performance was observed and recommendations on fattening concepts and final target weights in Fleckvieh bulls were provided. In Chapter 4, the analysis expands on the empty body tissue composition and chemical tissue composition in growing Fleckvieh bulls fed rations with different energy concentrations. The analysis should provide a better understanding of the breed's physiological capabilities. HE feed intake was expected to produce higher body fat content and fat accretion rates in Fleckvieh bulls, especially in high live weights.

To investigate the effect of NE and HE feed intake on growing Fleckvieh bulls, statistical analysis was performed using the mixed model (MIXED) procedure of the Statistical Analysis System (SAS, Version 9.4, SAS Institut, Cary, NC, USA). The corrected degrees of freedom were obtained using the Kenward-Roger method. The analysis included a two-way analysis of variance (ANOVA) with interaction (feed energy, weight group, feed energy x weight group). Differences between the groups were tested using the pairwise difference (PDIFF) option with effects stated as significant when $p < 0.05$. The results are presented as least square means (LSM) and the standard error of the mean (SEM).

In Chapter 4, results on empty body tissue composition and chemical composition in growing Fleckvieh bulls were used to calculate the body tissue, energy, and nutrient accretion rates in the animals. Thus, basic data for determining the nutrient and energy requirements of growing Fleckvieh bulls under different feeding conditions were provided. Furthermore, typical allometric growth patterns in body tissues and nutrients in growing Fleckvieh bulls were illustrated. For this purpose, third-order polynomial regression equations and their derivatives were used to calculate the gain composition and describe changes in the overall body proportions during the growth process. The regressions were modeled without intercepts because body components do not exist at a live weight of zero in the biological context. The regression analyses were calculated using the nonlinear (NLIN) procedure in SAS and based on the following model:

$$y_i = aLW_i + bLW_i^2 + cLW_i^3 + e_i$$

Where LW is the live weight and e is the residual error.

The results showed that animal body composition in both feed intake groups was equal at given live weights. Nonetheless, possible differences in the tissue and chemical content of gains had to be considered in the model. Therefore, the residuals of the fitted models for the NE and HE bulls were calculated to evaluate the goodness of fit of the regression equations since the most notable weaknesses in regression models are at the boundaries of the considered weight range. Furthermore, the calculated residuals were used to estimate significant differences between the feed intake groups. A two-way ANOVA showed no significant differences in the residuals of both feed intake groups. Hence, combined regression equations were calculated for both groups and presented in the results.

3 Influence of dietary energy concentration and body weight at slaughter on carcass tissue composition and beef cuts of modern type Fleckvieh (German Simmental) bulls

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The format of text, tables, figures, and references in this publication differ from the original article to ensure a uniform layout of this thesis. Tables have been inserted at the end of the publication.

Abstract

A feeding and slaughter experiment was conducted to evaluate the carcass tissue composition and meat quality of growing modern type Fleckvieh (German Simmental) bulls. For the study, 72 bulls were customary reared and for the fattening period allocated to a normal energy and a high energy treatment group with 11.6 and 12.4 MJ ME/kg DM, respectively. Bulls were slaughtered in a serial slaughter trial with final live weights of 120, 200, 400, 600, and 780 kg. The weights of carcasses, carcass quarters, beef cuts and their tissues (muscle, tendon, fat and bone) as well as meat quality traits were recorded. Results showed that carcass fat increased during growth primarily at the expense of bone and subsidiary muscle tissue, while the tendon content remained constant. Meat quality traits like IMF, meat color and tenderness were superior in high weight groups. Feeding high energy rations did not lead to increased fat accretion, but increased daily gain during certain stages of the fattening period.

Keywords

Beef cuts; Carcass composition; Fattening bulls; Feeding intensity; Meat quality

Author contributions

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.

Thomas Ettle: Conceptualization, Methodology, Supervision, Project administration, Writing-Review & Editing

3.1 Introduction

Studies on growth and tissue development of cattle (Augustini, Branscheid, Schwarz, & Kirchgeßner, 1992; Berg & Butterfield, 1976) indicated that the percentage of carcass meat and the proportion of beef cuts change during growth. Furthermore, the carcass tissue composition is subject to change, as each tissue reaches its growth maximum at a different point of maturity. Bone, as an early developing tissue, grows especially during fetal development and the first months of life. Extensive muscle growth is associated with increasing activity of the young animals, while accretion of fat tissue provides energy stores during later stages of development.

The Fleckvieh (German Simmental) breed is a common dual-purpose cattle breed in southern Germany and provides high milk and meat yields simultaneously. Fleckvieh is described as a late maturing cattle breed which can be fattened intensively to high final live weights and features high protein accretion (Augustini et al., 1992). Late maturing cattle breeds are associated with a slower physiological development in relation to their body weights and ages and possess a higher growth potential and slower fat accretion compared to early maturing cattle breeds (Irshad et al., 2013). Moreover, van der Westhuizen (2013) stated that late maturity leads to an increased growth of leaner carcasses because “Later maturing cattle will generally grow faster and will generally be better converters of high energy feed to carcass weight” (Van der Westhuizen, 2013). Hence, carcass traits of late maturing Fleckvieh bulls differ from those of early maturing Hereford cattle and the Holstein-Friesiean dairy breed as described by Keane (2011). Furthermore, the performance potential of late maturing Fleckvieh fattening bulls has been improved by selective breeding during the past decades, which may result in changes of fattening and slaughter traits of bulls fed with low and high concentrate rations, respectively.

The objective of this study was to specify the effects of dietary energy concentration and body weight at slaughter on carcass composition, carcass quarters, beef cuts and their tissue compositions as well as on meat quality of modern type Fleckvieh bulls.

3.2 Methods

3.2.1 Calf rearing

The experiment was conducted at the Bavarian State Research Center for Agriculture (LfL) according to European guidelines for animal experiments (Council Directive 2010/63/EU, 2010) and was approved by the ethics committee of the Ethics of Animal Experiments of LfL. For the study, 72 male Fleckvieh calves (German Simmental; age: 42d±9, body weight (BW) 80 kg±6) were randomly acquired from cattle farms in Bavaria, Southern Germany. The calves were randomly assigned to deep litter calf pens and fed with restricted amounts of milk replacer and *ad libitum* total mixed rations (TMR) according to Table 3.1 over a period of 6 weeks. The TMR for the period after weaning (8 weeks) was adjusted weekly and supplemented with brewer's yeast, 110 g per calf and day. 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.

3.2.2 Fattening period

For the fattening period, starting with an average BW of 225kg ±29 and age of 154d ±15, the bulls were randomly assigned to six beef pens housing 12 animals per pen. The pens were equipped with straw litter on sloped floors, automatic manure scrapers and automatic feed intake monitoring systems. The individual feed intake was recorded daily and BW was determined using a cattle scale in four-week intervals. Three pens each were allocated to a normal energy (NE) and a high energy (HE) treatment group with 11.6 and 12.4 MJ ME/kg DM, respectively. Crude protein contents per kg DM remained constant in both diets, while the HE treatment group was fed lower amounts of maize silage and more feedstuffs with higher energy density than the NE animal group. The compositions of NE and HE TMRs are illustrated in Table 3.2.

3.2.3 Feed analysis

The individual feed components were sampled and analyzed individually, while concentrates and TMRs were sampled weekly and pooled for a four week period. The analysis was performed using methods of VDLUFA (2012) for dry matter (DM, method 3.1), crude ash (CA, method 8.1), crude protein (CP, method 4.1.2), sugar (method 7.1.1) and neutral detergent fiber (aNDFom, method 6.5.1) determination. Additionally, by methods of the Commission Regulation EC No 152/2009, 2009, the content of crude fat (CF, method 152-H) and starch (method 152-L) was determined. The DM of maize silages was corrected for losses by oven drying according to Weißbach and Kuhla (1995) and the content of metabolisable energy (ME) was calculated from the individual analyses (DLG, 2011; GfE, 2008). The crude nutrient and energy content of the TMRs was calculated by their compositions and the crude nutrient and energy contents of the individual feed components.

3.2.4 Slaughtering and meat cutting

During the feeding trial, 5 target final live weights were set for slaughtering animals from both feeding groups: 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 bulls were separated from the group 20 h prior to slaughter, weighed and fasted from the TMR by feeding a hay and water diet for *ad libitum* intake in an isolation box. Slaughtering and meat cutting took place at the LfL Research Abattoir in Grub, Germany. The bulls were transported to the abattoir (distance 500 m), inspected by a veterinarian (ante-mortem inspection), weighed and held in lairage with free access to water until slaughter. Slaughtering was carried out in compliance with the Council Regulation EC No 1099/2009, 2009. The bull's final live weights were determined after stunning with a cattle gun and prior to bleeding. Dehiding, evisceration, carcass halving and trimming were carried out according to European standards (Commission Regulation EC No 1249/2008, 2008). Post-mortem inspection was performed by a veterinarian during the slaughtering process. Dressed carcasses (carcasses without inner organs, hanging tender, suet and body cavity fat) were weighed and chilled for 20 h at 4 °C. After chilling, the left and right side of each carcass were weighed as cold carcass weights and the right side of the carcass was dissected. To this effect, the carcass was quartered between the 8th and 9th rib, cut according to DLG cutting methods (Fig. 3.1; DLG, 1985) and each cut was manually dissected to muscle, tendon, fat and bone tissues. Each cut as well as the tissues of each cut were weighed separately.

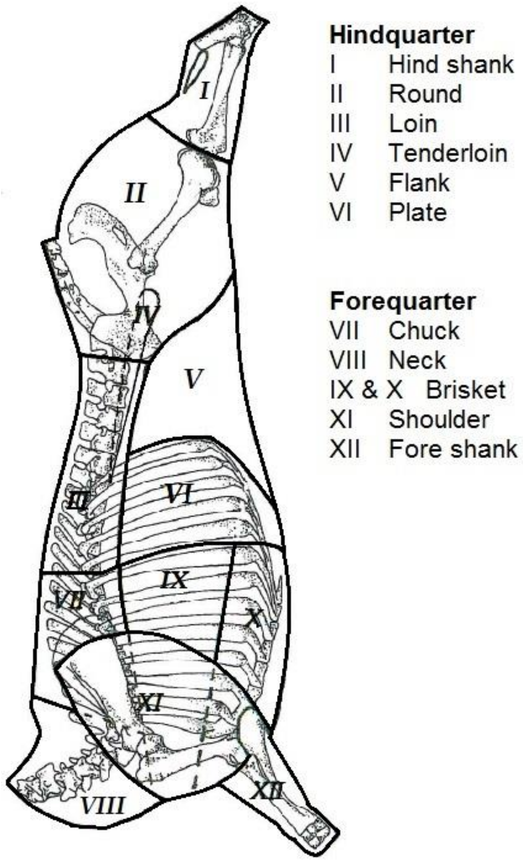

Figure 3.1: Beef cuts according to DLG cutting methods
(Figure modified from DLG, 1985).

3.2.5 Rib eye area and meat quality analysis

A sample of the Longissimus thoracis (LT) muscle (9th and 10th rib cut) was used for meat quality analysis. Muscle pH was measured using a portable pH meter (testo 205, Testo SE & Co. KGaA, Germany) 1 h, 24 h and 14 days after slaughtering. The rib eye area of the 9th rib was measured by digital image analysis and intramuscular fat (IMF) content was measured using petroleum ether in a Soxhlet extraction apparatus. Meat color was measured in CIELAB color space (L*: lightness, a*: redness, b*: yellowness), using a portable spectrophotometer (CM-508i, Minolta Camera CO., LTD., Japan). Ageing loss was recorded after storing the muscle sample from the 10th rib for 14d at 4 °C, cooking loss was determined after heating the 2.5 cm thick, stored sample in 70 °C warm water up to a meat core temperature of 70 °C. The shear force was measured after storing the cooked sample for 24 h at 4 °C, using the Warner-Bratzler method (2519-1kN, Instron GmbH, Germany).

3.2.6 Statistical analysis

Statistical analysis 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).

3.3 Results and discussion

3.3.1 Daily feed, energy and nutrient intake

As a consequence of feeding varying energy concentrations during the fattening period, HE treated bulls showed in all stages of the finishing period a higher daily DM, sugar, starch and energy intake than the NE animal group, while NE fed bulls showed a higher daily aNDFom intake (Table 3.3). Higher feed intake in the HE treatment group was most likely a result of increased concentrates proportion of the diet. Similar conclusions were drawn by Steen and Kilpatrick (2000), which fed varying amounts of concentrates to Simmental crossbred steers. Although crude protein contents of the NE and HE TMRs were identical, crude protein intake differed between the treatment groups because of the higher daily DM intake of HE fed bulls. However, crude protein intake of bulls in both treatment groups exceeded the bull's crude protein requirements (GfE, 1995) and therefore did not limit cattle growth.

3.3.2 Fattening performance

Feeding varying amounts of concentrates alters the daily weight gain, as was previously described by Slabbert, Campher, Shelby, Leeuw, and Kühn (1992) and Steen and Kilpatrick (2000). Further studies with Fleckvieh bulls fed with high energy diets found daily live weight gains of 1210 g/d for the fattening period in a weight range from 200 to 650 kg (Schwarz, Kirchgeßner, Augustini, & Branscheid, 1992) and peak live weight gain of

1536 g/d in a weight range of 205-363 kg (Schwarz & Kirchgessner, 1990). In the current study, the high energy ration led to average daily weight gains of 1699 and 1792 g/d for the NE and HE treatment group, respectively ($p < 0.1$). Peak live weight gains, with significantly higher gains of the HE treatment group, were reached in between 400 and 600 kg with 1753 and 1910 g/d in NE and HE treatment group, respectively (Table 3.3). Hence, bulls fed with high energy rations reached the target weight in shorter time.

While the target weights in the present study were kept comparable for NE and HE treatment groups, the slaughter ages of bulls in weight groups 600 and 780 kg differed between treatment groups (Table 3.4). The average slaughter age of HE bulls at 600 kg was 9 days less than those of NE bulls at the same weight. Likewise, HE bulls with final live weights of 780 kg were slaughtered 21 days earlier ($p < 0.05$) than NE bulls with same final weights. Comparison to former studies indicated an approximately 500 g higher daily weight gain of HE fed modern type Fleckvieh bulls than high energy fed bulls of past decades (Dannenberger, Nuernberg, Nuernberg, & Ender, 2006; Schwarz et al., 1992). Thus, present-day Fleckvieh bulls grow faster and reach final live weights of 600 kg approximately 130 days earlier than past decade bulls of the same breed when fed with high concentrates rations. The following results illustrate how the accelerated growth rates affected slaughter traits and carcass composition of modern type Fleckvieh bulls.

3.3.3 Dressing percentage and carcass tissues

The present data showed no significant effects of dietary energy concentration on dressing percentage, carcass composition and meat quality traits of NE and HE treatment groups. Hence, the combined results of both animal groups are shown.

With increasing body weight the dressing percentage increased from 52.2% to 59.7% ($p < 0.05$) in bulls with 120 kg and 780 kg final weights, respectively (Table 3.5). Comparison with previous studies showed that the dressing percentages of growing bulls in the present study were approximately 2% lower than in past decades Fleckvieh bulls with 650 kg final weight (Otto et al., 1994), but 3-4% higher than present Simmental bulls, steers and heifers (Coyne, Evans, & Berry, 2019; Sami, Augustini, & Schwarz, 2004; Terler, Velik, Kitzer, & Kaufmann, 2016). Hence, as a late maturing breed, modern type Fleckvieh converted feed energy efficiently into carcass growth.

Comparing the lowest and highest weight groups with 120 and 780 kg, carcass muscle percentage decreased by 4% ($p < 0.05$) while percentage of fat tissue increased by 13.6% ($p < 0.05$; Table 3.5). During the growth period, the percentage of bone tissue in the chilled carcasses decreased from 23.1% in 120 kg bulls to 13.2% in 780 kg bulls ($p < 0.05$). However, percentage of tendon did not vary between weight groups 120 and 780 kg with 6.0% and 5.9%, respectively. These changes in carcass tissue composition of growing Fleckvieh bulls are in line to results of Augustini et al. (1992) and Keane (2011) which concluded that growth alters the carcass composition of beef cattle. However, present data could not confirm former studies by Augustini et al. (1992), who observed differences in muscle and fat deposition between growing Fleckvieh bulls of a restricted and *ad libitum* feeding group.

In comparison, early maturing Hereford bulls featured lower dressing percentage (Bartoň, Řehák, Teslík, Bureš, & Zahrádková, 2006; Manninen, Honkavaara, Jauhiainen, Nykänen, & Heikkilä, 2011; Pesonen et al., 2013) while studies comparing Hereford and Simmental breeds indicate higher carcass fat proportion in Hereford and higher meat proportion in Simmental cattle (Bartoň et al., 2006; Mandell, Gullett, Wilton, Allen, & Kemp, 1998). The same effect could be observed by comparison with high yielding dairy cattle breeds as Holstein Friesian. This breed showed lower dressing percentage (Geuder, Pickl, Scheidler, Schuster, & Götz, 2012; Keane, 2011; Pfuhl et al., 2007) and carcass muscle tissue (Geuder et al., 2012; Keane, 2011), but higher carcass fat tissue percentage (Geuder et al., 2012; Keane, 2011) than Fleckvieh bulls. Overall, our data prove that late maturity leads to carcasses with a relatively high amount of muscle but low amount of fat, even in high weight groups.

3.3.4 Carcass quarters and tissues

Proportions of the carcass quarters remained constant throughout final live weights 120 and 200 kg, while the amount of the forequarter increased significantly at the expense of hindquarter portions in higher weight groups (Table 3.6). These observations, as well as the non-significant effect of the feed energy concentration on the amount of carcass quarters correspond to data reported from Augustini et al. (1992).

The majority of both carcass quarters consisted of muscle tissue, which decreased ($p < 0.05$) in the course of growth, particularly in the hindquarter, while tendon content decreased significantly in the forequarter and increased in the hindquarter. Furthermore, the percentage of bone tissue in the fore- and hindquarter decreased ($p < 0.05$) during growth by 11.6 and 8.8%, respectively, whereas the average amount of fat in the carcass quarters increased ($p < 0.05$) constantly up to 16.9% in the forequarter and 15.8% in the hindquarter. These observations are consistent with the *ad libitum* feed intake group of Augustini et al. (1992), which also showed higher fat accretion than bulls in the restricted feeding group. The shifts in quarter and tissue distribution characterize slow but progressive maturity of the fast growing bulls. Amounts of carcass quarters changed slightly, so valuable cuts of the hindquarter persisted in high final weights, as described in the next section.

3.3.5 Beef cuts and tissues

The following percentages of cuts and tissue composition of individual cuts are displayed in Table 3.7 and agree widely with data reported from Augustini et al. (1992) and Dannenberger et al. (2006). The share of cuts of the forequarter increased during growth, except for the front shanks. Fore and hind shank shares, as well as the round decreased in higher weight groups ($p < 0.05$). The percentage of muscle tissue in the individual cuts of beef decreased ($p < 0.05$) during growth except for neck, chuck and shanks. The greatest decrease of muscle tissue could be observed in the plate and flank, where muscle percentages decreased by 21.8 and 23.8%, respectively. Likewise, the percentage of bone tissue in all bone containing cuts decreased ($p < 0.05$) on average by 10% between 120 and 780 kg. The abatement of muscle and bone tissue is associated with an increasing proportion of fat tissue in all cuts ($p < 0.05$). Especially brisket, plate and flank showed high fat depositions of 24.7, 33.0 and 30.7%, respectively. Even the amount of tendons per cut changed during growth. Fore and hind shanks as well as loin and round showed increasing amounts of tendon tissue, while the tendon percentages of neck, brisket, plate and flank decreased in higher weight groups ($p < 0.05$). The growth of forequarter cuts is connected with progressive maturing of the bulls, but the late maturity of the breed slows down this process. Hence, valuable hindquarter cuts as loin and tenderloin showed the same proportions, even in high weight groups. As a consequence, the lean meat yield increased, because fat accretion increased only slowly while the amount of bone tissue decreased.

Significant differences between NE and HE feeding groups could be observed for the following particular cuts and their tissues. The neck percentage of HE bulls in weight group

400 kg was 0.6% higher ($p < 0.05$) than the NE treatment group. A reverse effect was detected in the 600 kg weight group, where the NE animals had 0.5% higher ($p < 0.05$) neck cut percentage, which is in agreement with data reported from Augustini et al. (1992). Another difference between both feeding groups became apparent for shoulder percentage in the 600 kg weight group, where HE fed bulls showed 0.7% higher ($p < 0.05$) shoulder percentage. Furthermore, the plate muscle percentage of the HE bulls in weight group 780 kg was 4% higher ($p < 0.05$) than those of the NE treatment group at the same final weight. Shoulder and loin of NE 400 kg bulls showed 1.5% and 1%, respectively, higher ($p < 0.05$) tendon percentage than the HE animal group. The fat and bone percentage of individual cuts showed no difference between treatment groups. Differences between feeding groups occurred mostly in forequarter cuts of high weight groups, which indicates that HE fed bulls matured slightly faster than bulls of the NE treatment group.

Data of Dannenberger et al. (2006) indicate significant higher neck, round and sirloin percentage in German Simmental compared to German Holstein bulls. Comparing studies which used the same cutting methods on Holstein-Friesian and Hereford carcasses, Holstein-Friesian showed higher loin, tenderloin and round percentage while subcutaneous fat yield of the round was superior in early maturing Hereford cattle (Huuskonen, Pesonen, Kämäräinen, & Kauppinen, 2013; Manninen et al., 2011; Pesonen et al., 2013). Comparison of dressing percentage and carcass composition with international studies that did not operate according to European Union standards is difficult, because carcass dressing procedures may differ between the countries and carcass cutting methods vary throughout all countries and regions.

3.3.6 Rib eye area and meat quality traits

Rib eye area and meat quality traits of growing modern type Fleckvieh bulls are displayed in Table 3.8. The rib eye area as well as the IMF content increased ($p < 0.05$) during growth up to 87cm2 and 3.3%, respectively. Comparison to former studies (Geuder et al., 2012; Sami et al., 2004) indicated a larger rib eye area of present bulls. The IMF content increased during the last decades (Schwarz & Kirchgessner, 1991), which is in agreement with data of Nuernberg et al. (2005) and Geuder et al. (2012). Meat color changed significantly during growth. The meat darkened, while redness intensified and yellowness decreased to 3.3 in 400 kg weight group and increased again in higher weight groups. The meat lightness widely corresponds to former studies (Nuernberg et al., 2005; Sami et al., 2004; Schwarz & Kirchgessner, 1991), but was lower than described by Terler, Velik, Kitzer, & Kaufmann, 2016. Meat redness and yellowness was consistent with data reported from Geuder et al. (2012), which processed the meat sample in the same way as in the present study, but lower than described by Sami et al. (2004) and Terler, Velik, Kitzer, & Kaufmann, 2016. Differences in meat color can occur through meat processing practices such as storage time and cooling and thereby pH value, but color is also influenced by time in lairage, nutrition, cattle breed and gender (Murray, 1989; Page, Wulf, & Schwotzer, 2001). The meat pH decreased within 24 h post mortem to an average of 5.5 and remained constant during 14d of cold storage. PH values 1 h and 24 h post mortem were in agreement with data reported from Geuder et al. (2012) and pH after 14d of storage consented with Sami et al. (2004). An average ageing loss of 5% was measured after 14d cold storage, which was higher than described in previous studies (Geuder et al., 2012; Sami et al., 2004). Cooking loss increased significantly in high weight groups and was comparable to data reported from Terler, Velik, Kitzer, & Kaufmann, 2016, but greater than described by Sami et al. (2004) and Geuder et al. (2012). Since IMF content in those studies was at a similar level, cooking loss seems to be independent of muscle IMF content. Former studies indicated that cooking loss can be altered by using variations of cooking or grilling methods and temperatures (Obuz, Dikeman, Grobbel, Stephens, & Loughin, 2004; Yancey, Apple, & Wharton, 2016). Concerning meat tenderness, high shear forces were measured in low weight groups, while 600 kg and 780 kg weight groups showed shear forces of 42.1 N and 46.0 N, respectively. Shear forces of animals in high weight groups were lower compared to former studies using the same cooking method, temperature and cattle breed (Geuder et al., 2012; Sami et al., 2004; Schwarz & Kirchgessner, 1991; Terler, Velik, Kitzer, & Kaufmann, 2016).

Regarding differences in cattle breeds, Holstein cattle used in studies by Geuder et al. (2012) showed smaller rib eye area, but higher IMF content. Differences in meat pH and meat lightness could not be observed, but meat tenderness was superior in Fleckvieh compared to Holstein cattle. The early maturing Hereford breed featured comparable meat pH, meat lightness and rib eye area, but higher IMF content and shear force (Papaleo Mazzucco et al., 2016; Pesonen et al., 2013). In summary, Longissimus thoracis of modern type Fleckvieh bulls showed larger rib eye area, but similar IMF content and meat lightness as previous studies on Fleckvieh bulls. Meat quality traits were characterized by higher ageing and cooking loss, but better tenderness compared to previous studies. Fattening Fleckvieh bulls to high final live weights of 780 kg had only a limited effect on IMF, but increased rib eye area and intensified meat color at consistently good tenderness.

3.4 Conclusion

Comparison with former studies indicates that modern type Fleckvieh bulls grow faster than bulls of past decades and the present study shows that feeding high energy rations shortens the fattening period for a high target weight as 780 kg. Since late maturing cattle breeds are efficient in exploiting high energy diets, only minor effects of the dietary energy concentration on carcass weights and the tissue compositions of carcass, quarters and cuts in NE and HE treatment groups were observed. The characteristics of a late maturing cattle breed became obvious during growth, when bulls produced large, lean carcasses with high muscle and low fat content. Percentage of fat in the carcasses increased primarily at the expense of bone and subsidiary muscle tissue, while the tendon content remained unchanged. Meat quality traits like IMF, meat color and tenderness increased in high final weight groups. Hence, fattening Fleckvieh bulls to high final weights as 780 kg can be recommended. In summary, modern type Fleckvieh bulls meet the needs of meat markets which target high production rates of lean beef.

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Declaration of Competing Interest

None.

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Tables

Table 3.1: Composition, crude nutrient and energy contents of feedstuffs fed during calf rearing.

Feedstuff	**Composition**		**Crude nutrients**					
	While milk feeding %DM	**After weaning** %DM	**DM** g/kg	**CA** g/kg DM	**CP** g/kg DM	**CF** g/kg DM	**aNDFom** g/kg DM	**ME** MJ/kg DM
Calf milk replacer (120 g/L)	5 L/d	–	961	69	210	191	0	16.6
Maize silage	–	63.6%	443	29	78	43	392	11.6
Hay	30.0%	3.7%	852	61	140	20	629	8.5
Molasses	14.3%	1.9%	775	209	108	0	0	10.9
Barley	17.7%	1.2%	879	23	98	20	154	13.0
Maize grain	11.1%	7.1%	888	14	98	42	82	13.3
Rapeseed meal	13.4%	14.2%	889	90	360	45	363	11.6
Pressed beet pulp	11.1%	6.2%	902	80	96	7	418	11.6
Soybean oil	0.3%	0.8%	999	0	0	999	0	30.6
Minerals, 26% Ca, 2% P	1.7%	1.1%	981	981	0	0	0	0
Calcium Carbonate	0.4%	0.3%	997	997	0	0	0	0
Brewer’s yeast	–	110 g/d	928	59	280	25	431	12.4

Table 3.2: Composition, crude nutrient and energy contents of feedstuffs fed for the fattening period.

Feedstuff	**Composition**		**Crude nutrients**					
	Normal energy %DM	**High energy** %DM	**DM** g/kg	**CA** g/kg DM	**CP** g/kg DM	**CF** g/kg DM	**aNDFom** g/kg DM	**ME** MJ/kg DM
Maize silage	80.0%	40.0%	355	31	77	34	336	11.8
Wheat	0.5%	15.5%	888	21	169	16	132	13.3
Maize grain	–	20.6%	889	13	91	41	94	13.3
Rapeseed meal	16.4%	16.7%	891	85	380	39	337	11.7
Pressed beet pulp	0.9%	5.5%	893	96	89	4	408	11.5
Feed grade urea 46,5% N	0.5%	–	990	0	2906	0	0	0
Minerals 26% Ca, 2% P	0.8%	0.8%	981	981	0	0	0	0
Calcium Carbonate, cattle salt	0.8%	0.8%	994	994	0	0	0	0

Table 3.3: Daily feed, nutrient, energy intake and weight gain of bulls in normal and high energy treatment groups in different weight ranges.

Feed intake/ fattening performance	**Weight range**								**SEM**	**p-value**		
	80-120 kg	**120-200 kg**	**200-400 kg**		**400-600 kg**		**600-780 kg**			Feed	Weight	Feed x weight
			NE	HE	NE	HE	NE	HE				
	n = 72	n = 64	n = 27	n = 27	n = 18	n = 18	n = 9	n = 9				
DM (kg/d)	1.92	4.38	7.03^{A}	7.75^{B}	9.47^{A}	10.66^{B}	10.72^{A}	11.35^{B}	0.09	<0.0001	<0.0001	<0.0001
CP (g/d)	321	647	1001^{A}	1107^{B}	1372^{A}	1546^{B}	1538^{A}	1665^{B}	11.91	<0.0001	<0.0001	<0.0001
aNDFom (g/d)	450	1464	2274^{A}	1973^{B}	3116^{A}	2701^{B}	3526^{A}	2759^{B}	28.87	<0.0001	<0.0001	<0.0001
Starch (g/d)	349	1245	2233^{A}	3276^{B}	2802^{A}	4419^{B}	3208^{A}	4769^{B}	36.68	<0.0001	<0.0001	<0.0001
Sugar (g/d)	358	229	208^{A}	286^{B}	257^{A}	357^{B}	292^{A}	398^{B}	4.20	<0.0001	<0.0001	<0.0001
ME (MJ/d)	24.6	51.4	82.1^{A}	96.1^{B}	110.1^{A}	132.3^{B}	124.3^{A}	141.7^{B}	1.02	<0.0001	<0.0001	<0.0001
Daily weight gain (g/d)	980	1452	1717^{A}	1841^{B}	1753^{A}	1910^{B}	1500	1521	27.07	0.0139	<0.0001	0.0407

Means within a weight range sharing the same superscript are not significantly different

Table 3.4: Animal performance of bulls in different treatment of energy density and slaughter groups.

Animal performance	**Slaughter group**								**SEM**	**p-value**		
	120 kg	**200 kg**	**400 kg**		**600 kg**		**780 kg**			Feed	Weight	Feed x weight
			NE	HE	NE	HE	NE	HE				
	n = 8	n = 10	n = 9	n = 9	n = 9	n = 9	n = 9	n = 9				
Slaughter age (d)	94	147	271	271	375	366	502^{A}	481^{B}	5.50	0.1744	<0.0001	0.5561
Final live weight (kg)	121	200	399	401	595	595	777	784	4.05	0.6334	<0.0001	0.9597
Warm carcass weight (kg)	63	105	228	226	345	352	469	462	2.84	0.9257	<0.0001	0.3701
Cold carcass weight (kg)	61	102	224	220	339	346	463	456	2.74	0.9357	<0.0001	0.2304

Means within a slaughter group with different superscripts differ significantly

Table 3.5: Average dressing percentage and carcass tissue composition of bulls in different slaughter groups.

Carcass	**Slaughter group**					**SEM**	**p-value**		
	120 kg n = 8	**200 kg** n = 10	**400 kg** n = 18	**600 kg** n = 18	**780 kg** n = 18		Feed	Weight	Feed x weight
Dressing percentage	52.2^{A}	52.7^{A}	56.7^{B}	58.5^{C}	59.7^{D}	0.44	0.4784	<0.0001	0.0510
Muscle	67.5^{A}	67.8^{A}	67.2^{A}	65.3^{B}	63.5^{C}	0.52	0.6566	<0.0001	0.7231
Tendon	6.0^{AB}	5.9^{B}	6.4^{A}	6.1^{AB}	5.9^{B}	0.15	0.2388	0.0683	0.5784
Fat	2.7^{A}	6.0^{B}	9.1^{C}	12.7^{D}	16.3^{E}	0.56	0.9888	<0.0001	0.6179
Bone	23.1^{A}	19.6^{B}	16.5^{C}	15.0^{D}	13.2^{E}	0.22	0.8211	<0.0001	0.4754

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

Table 3.6: Average percentages of carcass quarters and quarter tissues of bulls in different slaughter groups.

Carcass quarters		**Slaughter group**					**SEM**	**p-value**		
		120 kg n = 8	**200 kg** n = 10	**400 kg** n = 18	**600 kg** n = 18	**780 kg** n = 18		Feed	Weight	Feed x weight
Forequarter	Proportion	43.8^{A}	43.3^{A}	45.4^{B}	46.5^{C}	47.4^{D}	0.25	0.8573	<0.0001	0.7913
	Muscle	64.8^{A}	64.7^{AB}	65.4^{A}	64.9^{A}	63.1^{B}	0.54	0.7447	0.0166	0.9688
	Tendon	6.0^{A}	5.9^{A}	6.1^{A}	5.2^{B}	5.3^{B}	0.18	0.4936	0.0001	0.2320
	Fat	3.1^{A}	7.1^{B}	9.9^{C}	13.3^{D}	16.9^{E}	0.55	0.8456	<0.0001	0.7521
	Bone	25.7^{A}	21.9^{B}	18.2^{C}	16.2^{D}	14.1^{E}	0.25	0.8636	<0.0001	0.5842
Hindquarter	Proportion	56.2^{A}	56.7^{A}	54.6^{B}	53.5^{C}	52.5^{D}	0.25	0.7366	<0.0001	0.7916
	Muscle	70.0^{A}	70.5^{A}	69.1^{A}	66.2^{B}	64.4^{C}	0.55	0.6595	<0.0001	0.5576
	Tendon	6.1^{A}	6.0^{A}	6.7^{B}	6.9^{B}	6.6^{B}	0.16	0.1721	0.0007	0.9614
	Fat	2.4^{A}	5.2^{B}	8.6^{C}	12.3^{D}	15.8^{E}	0.60	0.8867	<0.0001	0.5160
	Bone	21.2^{A}	17.9^{B}	15.2^{C}	14.0^{D}	12.4^{E}	0.23	0.5490	<0.0001	0.4392

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

Table 3.7: Average percentages of beef cuts and tissue composition of cuts of bulls in different slaughter groups.

Beef cuts		**Slaughter group**					**SEM**	**p-value**		
		120 kg n = 8	**200 kg** n = 10	**400 kg** n = 18	**600 kg** n = 18	**780 kg** n = 18		Feed	Weight	Feed x weight
Neck	Proportion	7.2^{A}	6.8^{A}	7.8^{B}	7.8^{B}	8.1^{B}	0.15	0.9428	<0.0001	0.0326
	Muscle	66.8^{A}	69.1^{B}	73.2^{C}	75.6^{D}	74.2^{CD}	0.63	0.2846	<0.0001	0.6483
	Tendon	4.9^{A}	4.1^{AB}	3.6^{B}	2.6^{C}	2.8^{C}	0.28	0.7939	<0.0001	0.1529
	Fat	3.3^{A}	6.4^{B}	7.4^{B}	9.0^{C}	11.7^{D}	0.54	0.4089	<0.0001	0.8127
	Bone	24.8^{A}	20.0^{B}	15.3^{C}	12.4^{D}	11.0^{E}	0.46	0.9024	<0.0001	0.6136
Chuck	Proportion	9.3^{A}	8.8^{A}	9.8^{B}	10.5^{C}	10.9^{D}	0.16	0.6468	<0.0001	0.4763
	Muscle	68.2	69.7	68.8	69.2	68.1	0.61	0.9393	0.3650	0.8239
	Tendon	4.5^{A}	4.6^{A}	5.4^{B}	4.4^{A}	4.3^{A}	0.22	0.0380	0.0015	0.8108
	Fat	2.4^{A}	4.5^{B}	7.6^{C}	9.9^{D}	13.5^{E}	0.55	0.8910	<0.0001	0.8083
	Bone	24.4^{A}	20.6^{B}	17.7^{C}	16.0^{D}	13.4^{E}	0.47	0.5051	<0.0001	0.5922
Shoulder	Proportion	13.7^{AB}	13.3^{A}	14.0^{B}	14.5^{C}	14.4^{C}	0.15	0.7863	<0.0001	0.0579
	Muscle	70.6^{A}	68.6^{AB}	69.2^{AB}	68.2^{B}	66.1^{C}	0.61	0.3798	<0.0001	0.9806
	Tendon	6.6	6.5	7.4	6.9	7.3	0.36	0.3569	0.2756	0.0206
	Fat	2.6^{A}	7.0^{B}	8.7^{C}	12.1^{D}	14.9^{E}	0.62	0.2989	<0.0001	0.7465
	Bone	20.1^{A}	18.0^{B}	14.6^{C}	12.7^{D}	11.6^{E}	0.24	0.4394	<0.0001	0.2563
Brisket	Proportion	8.8^{A}	10.2^{B}	10.5^{BC}	10.6^{C}	11.2^{D}	0.16	0.4213	<0.0001	0.2861
	Muscle	63.3^{A}	61.4^{A}	58.2^{B}	54.3^{C}	51.2^{D}	0.82	0.6709	<0.0001	0.6352
	Tendon	4.8^{A}	4.4^{A}	4.5^{A}	2.8^{B}	2.8^{B}	0.36	0.0605	<0.0001	0.0732
	Fat	5.9^{A}	12.9^{B}	18.3^{C}	25.0^{D}	30.6^{E}	0.93	0.4867	<0.0001	0.4755
	Bone	25.0^{A}	20.5^{B}	18.5^{C}	17.4^{D}	14.8^{E}	0.35	0.3571	<0.0001	0.8667

Fore shank	Proportion	4.6^{A}	4.1^{B}	3.2^{C}	2.9^{D}	2.6^{E}	0.05	0.2959	<0.0001	0.7501
	Muscle	40.7	42.3	42.8	42.5	42.1	0.69	0.5604	0.3826	0.8479
	Tendon	11.0^{A}	12.8^{AB}	14.0^{BC}	14.8^{C}	16.3^{D}	0.56	0.2026	<0.0001	0.8896
	Fat	0.0^{A}	0.2^{A}	0.4^{A}	1.4^{B}	2.4^{C}	0.29	0.7590	<0.0001	0.9208
	Bone	47.7^{A}	43.6^{B}	42.2^{B}	40.5^{C}	38.6^{D}	0.65	0.7468	<0.0001	0.7870
Loin	Proportion	7.9^{A}	8.0^{A}	8.1^{AB}	8.3^{B}	8.1^{AB}	0.12	0.8930	0.1015	0.8857
	Muscle	64.7^{AB}	65.7^{A}	65.6^{A}	63.9^{B}	62.7^{B}	0.65	0.9742	0.0022	0.9734
	Tendon	4.3^{A}	3.9^{A}	6.5^{B}	6.2^{B}	6.1^{B}	0.33	0.6956	<0.0001	0.1515
	Fat	1.7^{A}	4.7^{B}	6.9^{C}	9.9^{D}	13.9^{E}	0.58	0.5780	<0.0001	0.4892
	Bone	28.5^{A}	25.1^{B}	20.2^{C}	19.2^{C}	16.5^{D}	0.59	0.4194	<0.0001	0.6383
Tenderloin	Proportion	2.1^{A}	2.3^{B}	2.2^{BC}	2.1^{AC}	2.1^{A}	0.04	0.7084	0.0022	0.9728
	Muscle	90.8^{A}	86.9^{B}	85.7^{B}	82.5^{C}	80.6^{D}	0.77	0.8082	<0.0001	0.7338
	Tendon	4.0^{A}	5.0^{B}	4.5^{AB}	3.8^{A}	4.0^{A}	0.29	0.2224	0.0426	0.4537
	Fat	4.3^{A}	7.6^{B}	9.4^{B}	13.1^{C}	14.7^{C}	0.71	0.5446	<0.0001	0.3892
	Bone	–	–	–	–	–	–	–	–	–
Plate	Proportion	3.9^{A}	5.0^{B}	6.0^{C}	6.5^{D}	7.2^{E}	0.16	0.6291	<0.0001	0.5411
	Muscle	73.8^{A}	71.9^{A}	64.8^{B}	57.1^{C}	52.0^{D}	1.20	0.8204	<0.0001	0.1278
	Tendon	8.9^{AB}	9.6^{A}	7.7^{B}	4.8^{C}	4.6^{C}	0.57	0.7573	<0.0001	0.5698
	Fat	1.7^{A}	6.1^{A}	16.8^{B}	28.1^{C}	34.7^{D}	1.36	0.7783	<0.0001	0.1523
	Bone	14.5^{A}	11.6^{B}	10.1^{C}	9.4^{C}	8.2^{D}	0.44	0.3505	<0.0001	0.9345
Flank	Proportion	3.0^{A}	3.3^{AB}	3.6^{B}	4.2^{C}	4.3^{C}	0.16	0.9061	<0.0001	0.9863
	Muscle	76.1^{A}	68.5^{B}	62.0^{C}	55.4^{D}	52.3^{D}	1.32	0.2247	<0.0001	0.4275
	Tendon	19.1^{A}	15.3^{B}	14.5^{B}	13.6^{BC}	12.1^{C}	0.79	0.6192	<0.0001	0.6126
	Fat	4.2^{A}	15.7^{B}	23.0^{C}	30.3^{D}	34.9^{E}	1.55	0.4572	<0.0001	0.6098
	Bone	–	–	–	–	–	–	–	–	–

Round	Proportion	31.3^{A}	30.9^{A}	29.2^{B}	27.2^{C}	26.4^{D}	0.19	0.3449	<0.0001	0.1451
	Muscle	76.6^{A}	76.8^{A}	75.6^{A}	73.7^{B}	72.8^{B}	0.48	0.4641	<0.0001	0.8470
	Tendon	3.1^{A}	2.9^{A}	4.0^{B}	4.9^{C}	4.7^{C}	0.22	0.1709	<0.0001	0.7325
	Fat	2.9^{A}	5.1^{B}	7.1^{C}	8.5^{D}	10.8^{E}	0.50	0.9113	<0.0001	0.7968
	Bone	17.3^{A}	15.2^{B}	13.3^{C}	12.9^{C}	11.7^{D}	0.19	0.5767	<0.0001	0.2428
Hind shank	Proportion	7.8^{A}	7.0^{B}	5.3^{C}	4.9^{D}	4.3^{E}	0.10	0.2301	<0.0001	0.3698
	Muscle	39.4^{A}	42.6^{BC}	40.9^{AD}	42.9^{C}	41.4^{BD}	0.54	0.2200	0.0004	0.7864
	Tendon	13.6^{A}	15.3^{AB}	16.1^{BC}	17.3^{CD}	18.1^{D}	0.63	0.4213	0.0001	0.3043
	Fat	0.0^{A}	0.9^{AB}	1.4^{B}	3.5^{C}	5.5^{D}	0.46	0.7306	<0.0001	0.7989
	Bone	46.2^{A}	40.5^{B}	40.9^{B}	35.5^{C}	34.2^{C}	0.59	0.5791	<0.0001	0.7223

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

Table 3.8: Rib eye area and meat quality traits of bulls in different slaughter groups.

Rib eye area and meat quality traits	**Slaughter group**					**SEM**	**p-value**		
	120 kg n = 8	**200 kg** n = 10	**400 kg** n = 18	**600 kg** n = 18	**780 kg** n = 18		Feed	Weight	Feed x weight
Rib eye area (cm²)	20.7^{A}	30.2^{B}	53.8^{C}	74.2^{D}	87.0^{E}	2.31	0.6361	<0.0001	0.5515
pH, 1h	6.8	6.8	6.8	6.8	6.8	0.05	0.2869	0.9418	0.1543
pH, 24h	5.6^{A}	5.6^{A}	5.5^{B}	5.4^{B}	5.4^{B}	0.02	0.2659	0.4179	0.6458
pH, 14d	5.6	5.6	5.6	5.5	5.5	0.02	0.4962	0.4537	0.4183
IMF (%)	0.5^{A}	0.7^{A}	1.3^{B}	2.4^{C}	3.3^{D}	0.20	0.4108	<0.0001	0.7271
Ageing loss, 14d (%)	4.9^{AB}	5.8^{A}	4.6^{B}	4.8^{B}	5.1^{AB}	0.31	0.2410	0.0775	0.5646
Cooking loss (%)	26.0^{A}	27.4^{A}	29.7^{B}	30.6^{B}	30.7^{B}	0.76	0.3539	0.0002	0.9576
Shear force (N)	61.9^{A}	86.5^{B}	49.2^{C}	42.1^{C}	46.0^{C}	3.79	0.7912	<0.0001	0.4233
Meat color									
L*	42.2^{A}	42.0^{A}	37.2^{B}	36.9^{B}	34.6^{C}	0.56	0.4147	<0.0001	0.1774
a*	5.8^{A}	4.6^{A}	8.9^{B}	11.0^{C}	13.2^{D}	0.49	0.6723	<0.0001	0.8162
b*	4.5^{A}	3.6^{AB}	3.3^{B}	4.6^{A}	4.2^{A}	0.37	0.6269	0.0341	0.2603

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

4 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.

Keywords

Body composition; Body tissues; Chemical composition; Fattening bulls; Feeding intensity; Growth

Author contributions

Aniela C. Honig: Investigation, Data Curation, Formal analysis, Writing-Original Draft.

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Hubert Spiekers: Resources, Supervision, Writing-Review & Editing.

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Kay-Uwe Götz: Funding acquisition, Writing-Review & Editing.

Manfred Schuster: Formal analysis, Validation, Data curation.

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4.1 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 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.

4.2 Materials and methods

4.2.1 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).

4.2.2 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.

4.2.3 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.

4.2.4 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).

4.3 Results and discussion

4.3.1 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.

4.3.2 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 4.1. 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 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.

4.3.3 Chemical composition of the empty body and body tissues

The chemical contents and related regressions are illustrated in Fig. 4.1. 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 4.2). 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 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.

4.3.4 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 4.3, Fig. 4.2), 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 4.3, Fig. 4.3) 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). 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.

4.3.5 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.

4.4 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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Tables

Table 4.1: 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.

Table 4.2: 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.

Table 4.3: 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

Figures

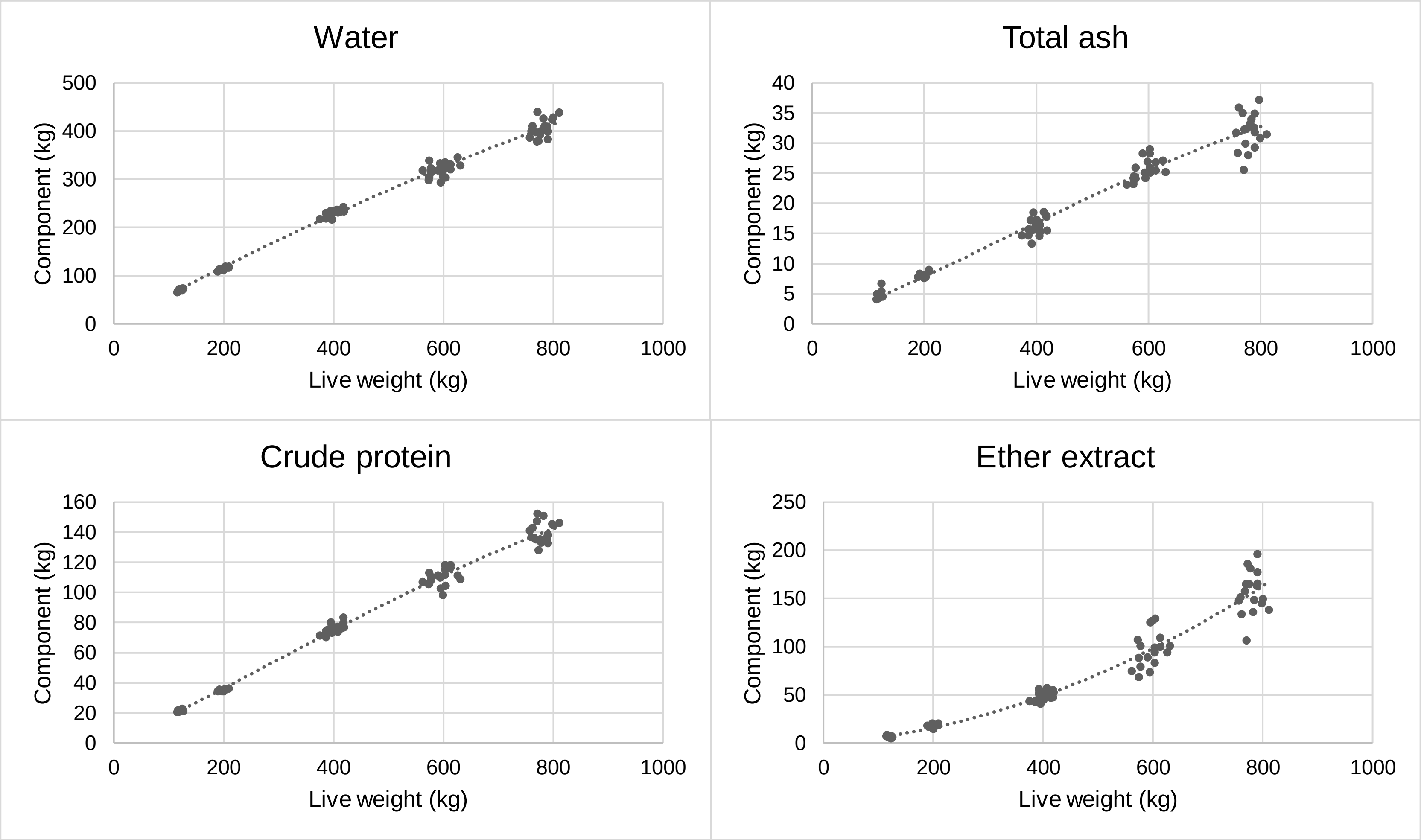

Figure 4.1: Chemical body components of bulls with different live weights.

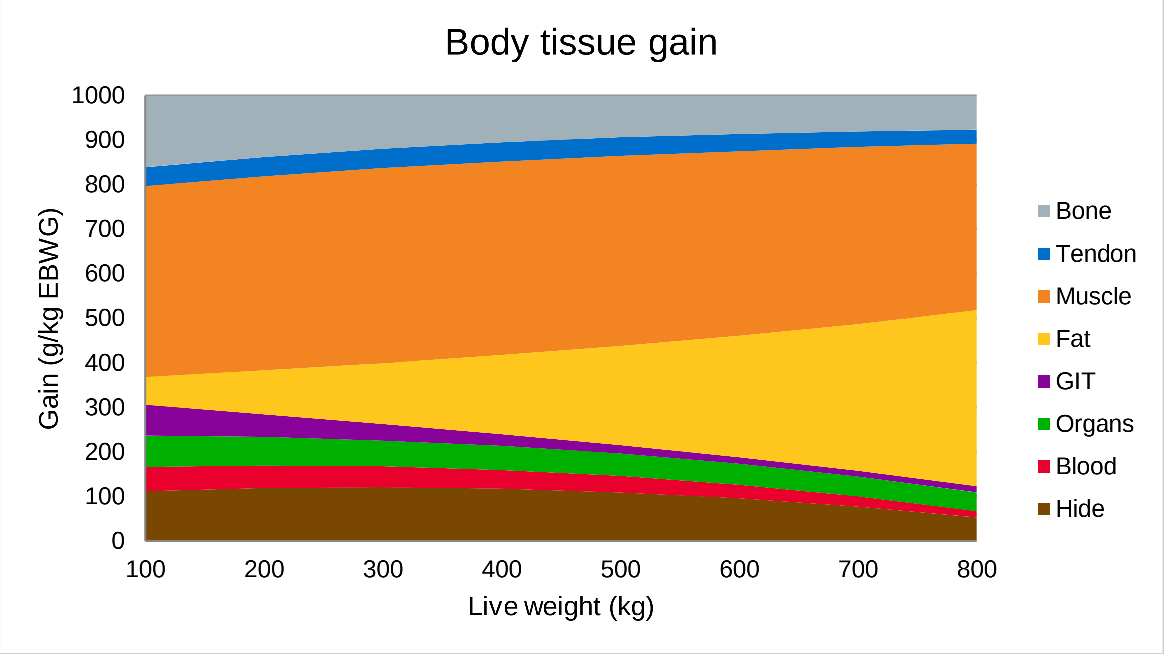

Figure 4.2: Calculated body tissue gain per kg empty body weight gain.

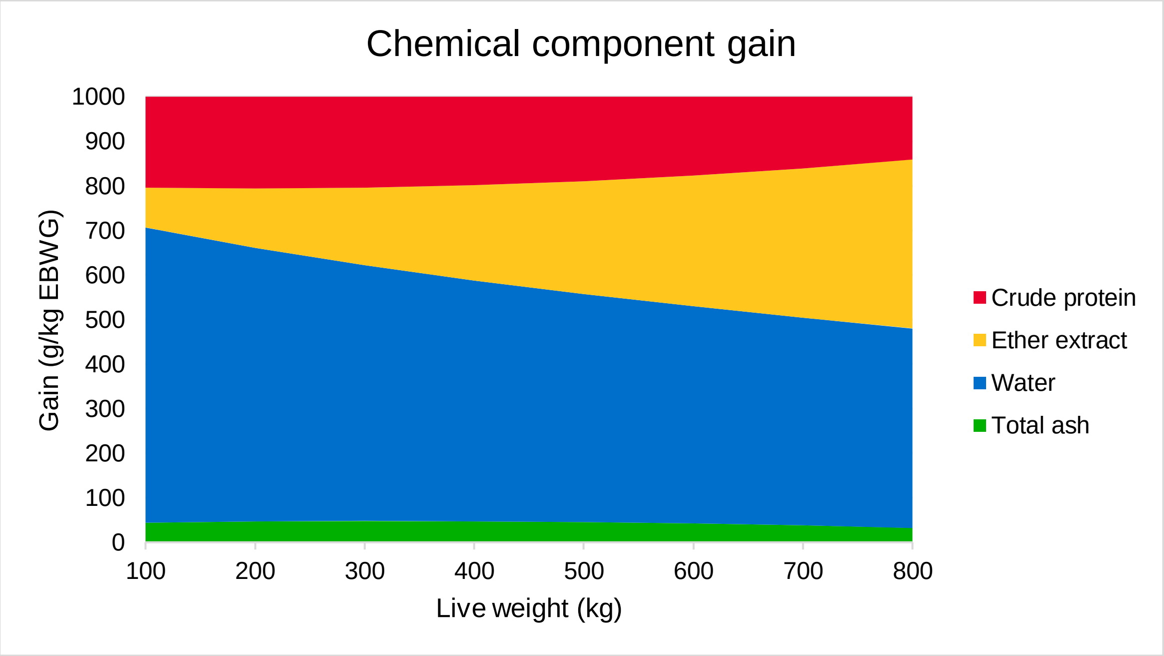

Figure 4.3: Calculated chemical component gain per kg empty body weight gain.

Supplementary material

Table 4.4: Parameters for regression equations on empty body mass, body tissues and chemical components.

Regression equation: $y = aLW_i + bLW_i^2 + cLW_i^3 + e_i$					
y	**Estimated parameter**			**SE**	**R^2**
	a	**b**	**c**		
Empty body weight	0.8557 ± 0.0167	0.000205 ± 0.00006	-1.25E-07 ± 5.198E-08	6.60	0.9991
Hide	0.0819 ± 0.00821	0.000094 ± 0.00003	-9.61E-08 ± 2.561E-08	3.25	0.9811
Blood	0.0467 ± 0.00482	0.000003955 ± 0.000017	-2.11E-08 ± -1.502E-08	1.91	0.9484
Organs	0.0659 ± 0.00472	-0.00002 ± 0.000017	2.493E-09 ± 1.471E-08	1.87	0.9759
GIT	0.0778 ±0.00638	-0.00009 ± 0.000023	4.087E-08 ± 2.016E-08	2.51	0.8787
Fat	0.0222 ± 0.0305	0.000154 ± 0.00011	4.792E-08 ± 9.509E-08	12.08	0.9414
Muscle	0.3454 ± 0.027	0.000172 ± 0.000098	-1.46E-07 ± 8.414E-08	10.69	0.9871
Tendon	0.0333 ± 0.00433	0.000022 ± 0.000016	-2.09E-08 ± 1.351E-08	1.72	0.9650
Bone	0.1579 ± 0.00761	-0.00009 ± 0.000028	2.924E-08 ± 2.374E-08	3.02	0.9809
Ether extract	0.0358 ± 0.0349	0.000223 ± 0.000126	-1.63E-08 ± 1.087E-07	13.81	0.9410
Crude protein	0.1699 ± 0.0115	0.000076 ± 0.000041	-8.22E-08 ± 3.576E-08	4.54	0.9886
Total ash	0.0341 ± 0.00459	0.000031 ± 0.000017	-2.78E-08 ± 1.433E-08	1.82	0.9667
Water	0.616 ± 0.0289	-0.00012 ± 0.000105	1.513E-09 ± 9.029E-08	11.47	0.9907

LW: live weight; e: residual error

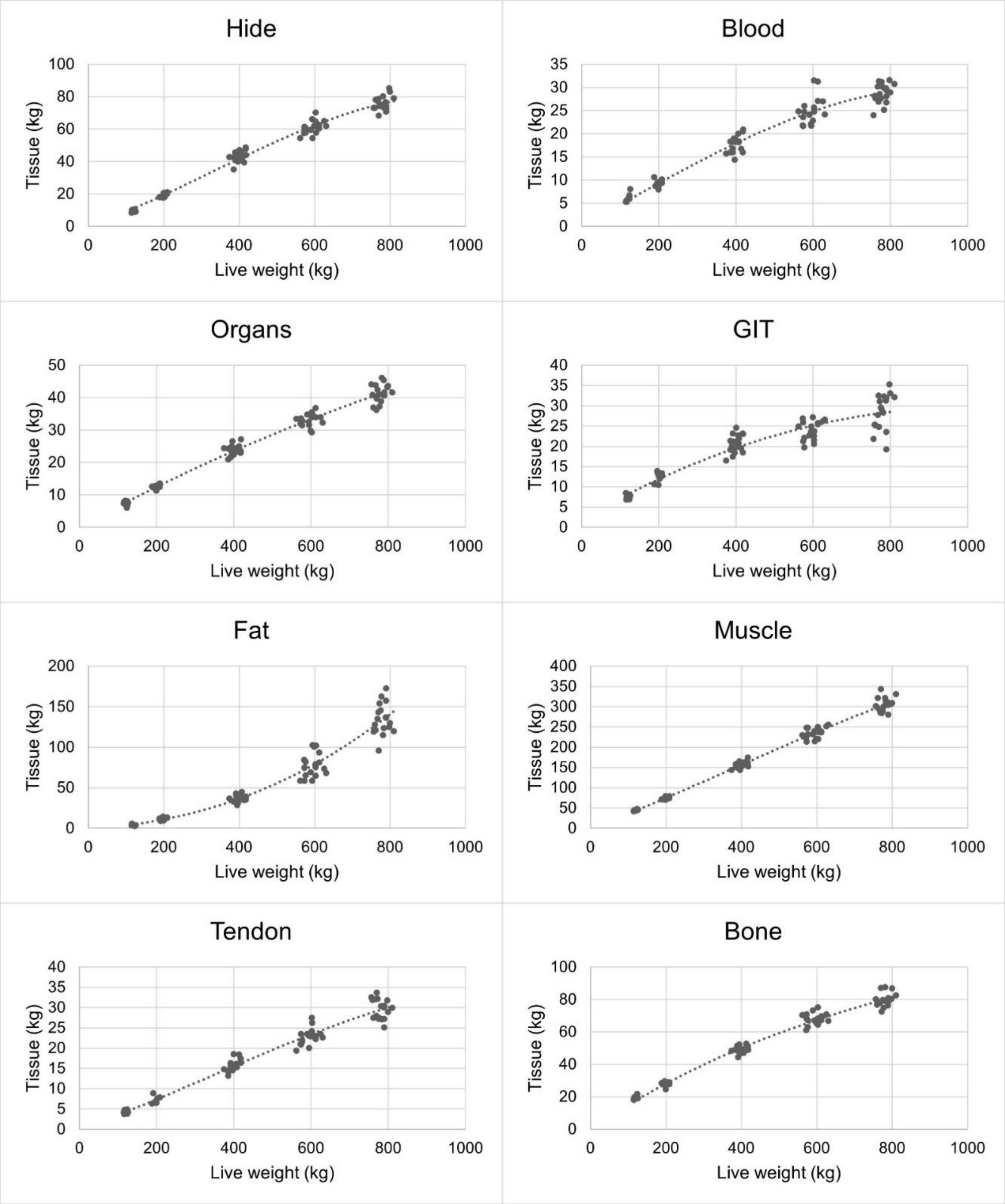

Figure 4.4: Contents of body tissues in bulls with different live weights.

5 General discussion

This comprehensive discussion interprets the results in Chapters 3 and 4 (Honig et al., 2020, 2022). The research project aimed to generate basic data for determining the nutrient and energy requirements of growing Fleckvieh bulls. Feeding recommendations must adequately reproduce the amount of energy and nutrients required to maintain physiological growth processes in cattle to ensure adequate growth performance. The performance potential of Fleckvieh cattle has been improved by selective breeding and progress in cattle farming and feeding during past decades. Hence, a major aspect of the study was to investigate whether the body composition and growth patterns of Fleckvieh bulls have changed and whether feeding cattle high energy rations influences growth.

In this study, feeding the animal groups varying energy concentrations should produce differences in fattening performance and body composition (Chapters 3 & 4). Previous research into the body composition of cattle under different feeding conditions showed that high-energy feed intake could lead to higher fat accretion (Steen & Kilpatrick, 2000). Excessive body and carcass fat tissue are undesirable for cattle farmers and the meat industry because consumers primarily pay for beef as the final product and not the fat tissue. Hence, cattle farmers select animals for slaughter at a particular stage of maturity, when the animals yield high-grade carcasses. In this context, it must be considered whether feeding Fleckvieh bulls high-energy rations leads to higher body fat accretion and carcasses with increased fat tissue and decreased lean meat content.

The results of this thesis presented in Chapters 3.3 and 4.3 revealed no significant differences in body composition, gain composition, carcass traits, and meat quality characteristics in NE- and HE-fed Fleckvieh bulls. Regardless of feed energy concentrations, current Fleckvieh bulls showed improved fattening performance (Chapter 3.3.2) compared to the bulls previously studied by Schwarz et al. (1992). Peak live-weight gains were achieved in the 400–600 kg weight range with daily weight gains of 1753 g and 1910 g in NE- and HE-fed bulls, respectively (Table 3.3). These daily weight gains are considerably higher than those recommended in the feeding guidelines for Fleckvieh beef cattle (GfE, 1995). Furthermore, peak weight gains in current Fleckvieh bulls reached a higher live-weight range than indicated in previous feeding recommendations (GfE, 1995). Hence, feeding recommendations must be regularly adjusted to reflect the current performance level of beef bulls.

5.1 Modeling the composition of gain to evaluate nutrients and energy requirements and illustrate ontogenetic allometry in cattle

An important step to generate basic data for determining the nutrient and energy requirements of Fleckvieh beef bulls was to determine the body composition and gain composition in growing bulls (Chapter 4), which can be used to illustrate allometric growth patterns in cattle.

Huxley (1924; 1932) used the function $y = bx^k$ to describe allometric animal growth, where y is the size or weight of a body component, x represents the body size or live weight, and b and k are constants. Instead of a power function, this study used a third-order polynomial regression of live weight to determine individual tissue contents and chemical components in the bull's bodies (Chapter 4). The first derivatives of the body composition functions characterized the expected gains in individual body fractions for a given live weight. The advantage of using third-order polynomials is the ability to derivate minima or maxima from the function. This process was necessary because power functions commonly used to describe allometric growth express the weight of a body part as a function of live weight and thus at a defined point in the animals' maturity. Nevertheless, they provide limited capacity for describing growth processes in specific body parts.

Ontogenetic allometry describes changes in body proportions due to growth processes in body parts and tissues, which develop at different stages of maturity and show distinct gain rates. Hence, a function describing allometric growth in animals must meet the following requirements: (1) describe the contents of body fractions at a given live weight during the animal's maturation process, (2) specify the gain rates of body fractions at a given live weight, and (3) adequately reflect changes in the growth rates of body fractions during the animal's maturation process.

The power function $y = bx^k$ meets the first requirement. However, the derivative lacks the ability to reproduce growth rate minima or maxima, which are important elements of allometric growth processes in different body parts and tissues. It is possible to describe the growth of a body fraction relative to the entire body using the constant k as a growth coefficient. However, it is not possible to describe the growth of a body part during animal maturation because the growth processes of body fractions include different developmental stages such as the beginning, peak, and slowing of development (Hammond, 1950). The different stages are specified by the body fractions' gain rates, which change during growth (Hammond, 1950). These changes cannot be entirely described using a power function or series of power functions. Therefore, a function that fully meets the requirements and describes the entire process of allometric growth in animals should be used. Third-order polynomial regressions and their derivatives fulfill the requirements; hence, they were used in this study (Chapter 4) to calculate the contents of body tissues and chemical components, as well as their rates of gain.

The described approach can also be used to calculate the gain rates of individual minerals and amino acids in growing cattle, which are expected to be influenced equally by allometric growth process. The results of energy and nutrient accretion in modern developing Fleckvieh bulls are essential to evaluate feeding recommendations within the calculated weight range. The weight range is a limiting factor because calculating nutrient accretions beyond the given weight range does not reflect actual growth processes in the animals.

In this thesis, accretion rates were calculated in Fleckvieh bulls ranging from 100–800 kg live weight with daily weight gains of 800–2000 g, reflecting the animals' current performance level. Daily accretion rates were calculated based on an EBWG to BWG relation of 0.95, as derived from the present study and was previously assumed by GfE (1995). Calculated rates of daily crude protein, crude fat, and energy accretion in Fleckvieh bulls with different live weights and daily body weight gains are displayed in Table 5.1. The results show that the accretion rates differ from those described in the GfE feeding recommendations (Table 1.1; GfE, 1995). Current Fleckvieh bulls featured lower protein but higher fat and energy accretion in high-weight groups. Furthermore, increased daily weight gains in HE-fed bulls were associated with higher daily energy and nutrient accretion rates. These findings indicate that feeding recommendations must be regularly adjusted to fit growing Fleckvieh bulls' performance levels and energy and nutrient requirements.

The protein accretion rate in growing bulls can also be used to calculate nitrogen accretion rates by dividing protein accretion by 6.25. Determining daily nitrogen intake and accretion in livestock provides information about the amount of nitrogen excreted per animal and day. This information becomes important when targeting a reduction in nitrogen excretions by farm animals. Reducing nitrogen excretions from farm animals can minimize the environmental impacts, which will be discussed further in the following chapters.

Table 5.1: Daily accretion rates of crude protein, crude fat, and energy in Fleckvieh bulls with different live weights and daily weight gains
(calculated based on data by Honig et al., 2022).

Daily live weight gain (g)	**Live weight (kg)**							
	100	**200**	**300**	**400**	**500**	**600**	**700**	**800**
	Crude protein accretion (g/d)							
800	155							107
1000	194	196					153	133
1200	233	235	232			202	183	160
1400		274	271	264	252	236	214	187
1600		313	310	302	288	269	245	
1800			349	339	324	303		
2000				377	360			
	Crude fat accretion (g/d)							
800	68							288
1000	85	126					319	360
1200	102	152	199			335	382	433
1400		177	232	285	337	391	446	505
1600		202	265	325	386	446	510	
1800			298	366	434	502		
2000				407	482			
	Energy accretion (MJ/d)							
800	6.2							13.7
1000	7.7	9.4					15.9	17.1
1200	9.2	11.2	13.0			17.6	19.1	20.5
1400		13.1	15.2	17.1	18.9	20.6	22.2	23.9
1600		15.0	17.3	19.5	21.5	23.5	25.4	
1800			19.5	21.9	24.2	26.4		
2000				24.4	26.9			

5.2 Illustrating patterns of allometric growth in body tissues and nutrients considering the cattle maturity type

The appropriate adjustment of feeding recommendations for beef bulls requires knowledge of the bulls' growth processes considering the breed's maturity type. In this study, allometric growth was evident in changes in carcass and body tissue distribution, as well as chemical tissue composition and the chemical composition of the growing bulls' bodies.

Ontogenetic allometry can be observed in changing body and carcass proportions in growing cattle. Results in Table 3.6 showed that in the carcass, the forequarter share increased during growth, while the hindquarter share decreased. This observation supports research conducted by Augustini et al. (1992) and is a result of different growth processes in individual body parts, which can be demonstrated in the growth of individual beef cuts. The forequarter proportion increased with body weight due to growth processes in the neck, chuck, shoulder, and brisket beef cuts (Table 3.7). Regarding the decreasing hindquarter proportion, Table 3.7 shows that growth processes in individual beef cuts led to increasing portions of plate and flank but decreasing amounts of the round. Allometric growth was evident in all beef cuts when the amount of early developing bone tissue decreased as the amount of late-developing fat tissue increased (Table 3.7). Furthermore, allometric growth advanced slowly because Fleckvieh bulls' carcasses featured high amounts of lean meat and relatively low amounts of fat tissue throughout all weight groups (Table 3.5).

Cattle body composition depends on the growth processes of different body tissues and nutrients. The tissue-growth results in Fleckvieh bulls (Table 4.3) allowed the classification of body tissues into early growing (bone, blood, organs, GIT), intermediate growing (hide, muscle, tendon), and late-growing tissues (fat), which corresponds with previous research into cattle growth (Hammond, 1950; Berg & Butterfield, 1968; Owens et al., 1993). The tissue-growth data for Fleckvieh bulls (Table 4.3) was used to draw a typical allometric growth pattern for different cattle body tissues, as illustrated in Figure 5.1. Early, intermediate, and late-growing tissues showed specific growth patterns related to the animal maturity stage. For Fleckvieh bulls, it was assumed that full maturity is achieved when bulls reach an average mature weight of 1200 kg (BLE, 2021).

Growth patterns in the respective tissue types, depending on the animals' relative stage of maturity (Figure 5.1), differed from the concept of cattle growth described by Hammond (1950) and discussed in the introduction of this thesis (Figure 1.1). The main difference is

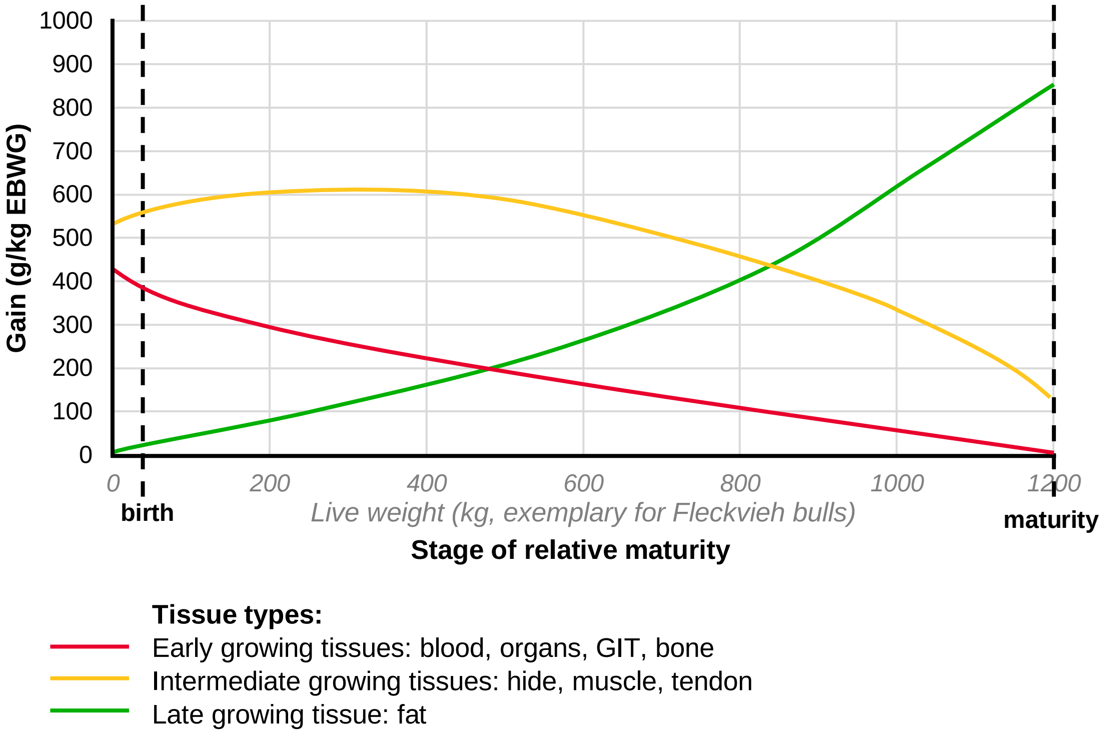

Figure 5.1: Typical pattern of tissue gain in cattle
(illustrated based on data by Honig et al., 2022).

that early growing tissues such as bone, blood, organs, and GIT reached their peak growth rates at the beginning or even before the weight range observed in this thesis. Thus, early growing tissues showed decreasing rates of gain during the maturation process. Intermediate growing tissues such as hide, muscle, and tendon reached their peak growth rates at 300 kg body weight, and their rates of gain declined afterward. Finally, late-growing fat tissue demonstrated increasing gain rates during the maturation process.

Developmental processes in body tissues are accompanied by changes in nutrient composition, as shown in Table 4.2. Hence, the nutrient-accretion data for Fleckvieh bulls (Table 4.3) can be used to draw a typical accretion sequence for individual nutrients in line with the body tissue types by classifying the nutrients into early, intermediate, and late-accumulating types, as illustrated in Figure 5.2. Water is considered an early accumulating nutrient because it reaches peak gain at the beginning of cattle growth when developmental processes start. Protein and ash are classified as intermediate accumulating nutrients because they reach peak gain when intermediate developing body tissues such as hide,

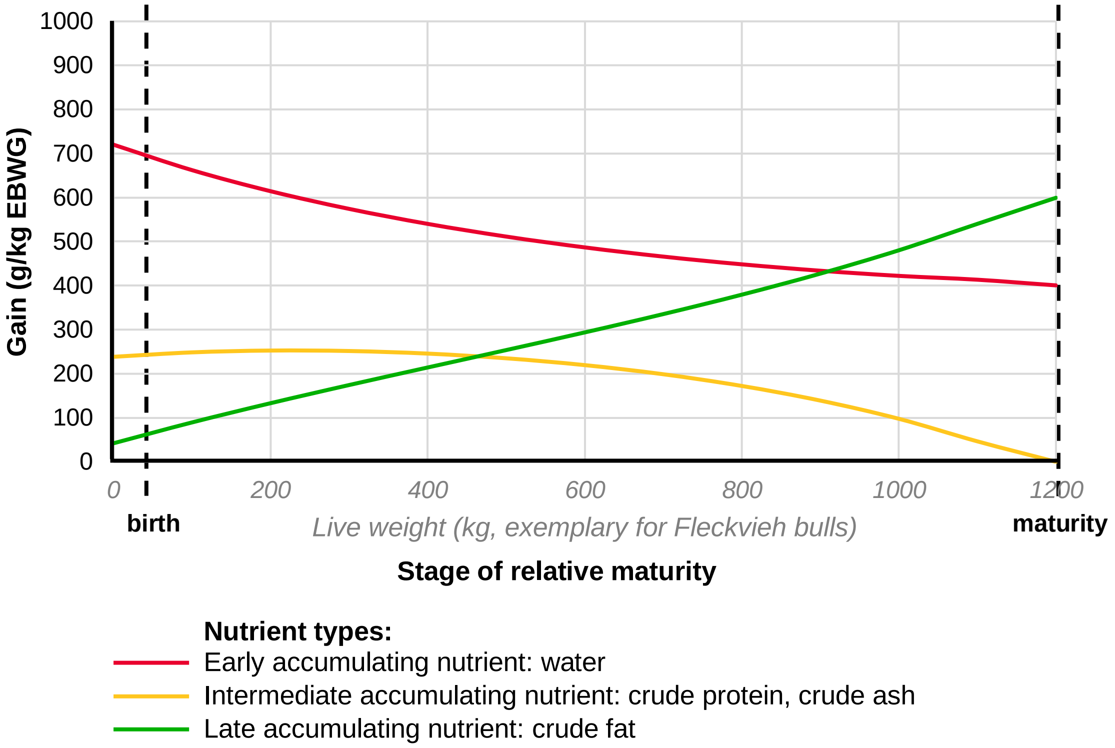

Figure 5.2: Typical pattern of nutrient gain in cattle
(illustrated based on data by Honig et al., 2022).

muscle, and tendons demonstrate their highest growth rates, while early developing tissues such as bone and organs are still in their developmental stage. In contrast, crude fat accretion increases continuously during growth, while crude fat is stored in fat cells for energy deposition. Thus, crude fat shows the highest rates of gain in the latest stage of cattle growth. Hence, it can be classified as a late-accumulating nutrient. The total amount of tissue and nutrient gain at a particular stage of maturity depends on the animals' actual daily weight gain, which was not considered in Figures 5.1 and 5.2.

Owens et al. (1993) stated that maturity is reached when maximum muscle proportion is attained. However, this statement cannot be confirmed because fat tissue growth progresses after this stage. Fat tissue development comprises crude fat deposition in fat cells (Robelin, 1981), accompanied by increasing body volume. Hence, intermediate growing hide tissue must continue to grow until fat deposition ends. Therefore, Owens et al.'s (1995) argument that maturity is attained when maximum body protein content is reached seems to be a better explanation. The definition of maturity based on ceasing protein gain can be confirmed by typical patterns of nutrient gain, illustrated in Figure 5.2. It can be further concluded that full animal maturity is reached when all body tissues have completed their development and ceased growth. The results of this thesis showed that beef bulls are slaughtered for meat production before they reach maturity. The time for slaughter is chosen at a stage of maturity when fat tissue gain exceeds muscle gain. This weight stage is reached at about 800 kg in Fleckvieh bulls (Table 4.3).

In terms of cattle maturity types, comparison of the empty body chemical composition in *ad libitum* fed late-maturing Fleckvieh bulls (Table 4.2) with *ad libitum* fed early-maturing Angus x Hereford crossbred steers in studies by Carstens et al. (1991) showed higher crude fat but lower water and protein content in early-maturing steers at defined live weights. Hence, Fleckvieh bulls exhibit slower fat accretion and decrease of water and protein proportions during growth. Furthermore, comparison of the body composition reveals that late-maturing Fleckvieh bulls with a 780 kg live weight (Table 4.2) show an empty body chemical composition comparable to that of early-maturing steers with a 325 kg live weight in research by Carstens et al. (1991). The comparison of early and late-maturing breeds clarifies why late-maturing beef cattle can be fattened intensively to high final weights.

Further studies based on this research project will analyze mineral and amino acid contents in growing Fleckvieh bulls. In this context, the previously described approach of categorizing tissues and nutrients into early, intermediate, and late-gaining components can be used to determine an accretion sequence for minerals and amino acids in growing bulls. The mineral and amino acid content in individual body tissues is expected to change during allometric growth due to progressive tissue development. Schulz et al. (1974) and Schwarz et al. (1995b) demonstrated changes in the mineral content of different body tissues in growing bulls. The most significant changes were observed in the mineral content of bone tissue, which can be attributed to the ossification process (Schulz et al., 1974; Schwarz et al., 1995b). Comparing the bone mineral content in late-maturing Fleckvieh bulls (200–650 kg live weight) with earlier maturing Schwarzbunte bulls (152–576 kg live weight) revealed higher bone mineral content in the earlier maturing bulls, especially in high final weights (Schulz et al., 1974; Schwarz et al., 1995b). These findings indicate faster tissue development in early maturing cattle.

In terms of amino acid composition, the concept of allometric growth implies that there cannot be a single first-limiting amino acid throughout the cattle growth process. The amino acid content in the body tissue fractions of calves differs from that in older beef cattle (Souci et al., 2008). Hence, the amounts of individual amino acids required for cattle growth are expected to change, depending on the development stages of different body tissues. To identify a first-limiting amino acid, the maturity stage, implying the stage of tissue growth, must be considered. For example, investigating a first-limiting amino acid in muscle growth would be most promising at peak muscle and protein gain. In Fleckvieh bulls, this would include animals with 200–300 kg live weight (Table 4.3). After this stage, the rates of protein accretion decrease steadily. Thus, experimental rations would have to be constantly adjusted, which complicates the research. The search for a first-limiting amino acid is further complicated by the different types of maturity in cattle. Vopálenský et al. (2017) demonstrated differences in the amino acid content of beef in different cattle breeds. Since early maturing cattle breeds exhibit faster physiological growth, they are expected to need more frequent adjustments in amino acid supply according to their growth stage. Therefore, late-maturing cattle breeds should be selected to observe the amino acid supply and the effects upon the growth of specific tissues over an extended trial period.

The sequence of tissue and nutrient growth can be used to adjust feeding recommendations according to the specific requirements of growing cattle. Feeding recommendations based on the live weights of cattle should enable cattle breeds and their respective maturity types to be differentiated. As an intermediate accumulating nutrient, crude protein reaches its peak gain at 200 kg live weight in Fleckvieh bulls (Table 4.3). After this peak, the protein supply can be steadily reduced by phase feeding, reducing nitrogen excretion from the animals. In early-maturing cattle breeds, a faster reduction in protein supply can be realized since physiological growth processes proceed more rapidly than in late-maturing cattle. Furthermore, early maturing cattle breeds show higher crude fat gain than late-maturing breeds at defined live weights. Higher fat gain is associated with increased energy accretion since crude fat contains more energy than crude protein. Thus, energy supply must be adequately adjusted to fat and protein gain in early and late-maturing cattle breeds to avoid delays in cattle growth. Overall, feeding recommendations must be geared to the animals’ physiological needs. A feeding concept that does not meet the requirements of high-performing beef cattle may decrease fattening performance by delaying allometric growth.

5.3 Using the study results to improve resource efficiency and environmental protection through sustainable feeding concepts

The sustainability of cattle feeding has a decisive role in future agricultural practices because livestock feed production competes with human food production for resources such as land, water, and energy. In particular, the cultivation of high-quality feedstuffs (e.g., wheat, soya beans, and maize) for use as concentrates in cattle feeding competes directly with human nutrition. These crops can only be grown on suitable arable land. However, considerable portions of agricultural land are located in areas unsuitable for high-quality crop production, for geographical or meteorological reasons. Nonetheless, most land unsuitable for arable farming can contribute to human nutrition by being primarily used as grasslands for grazing livestock. Furthermore, ruminants can metabolize non-edible crops that are part of crop rotation and cannot be used for human nutrition. Accordingly, the physiological advantages of ruminants should be exploited more in the future. Increasing the proportion of roughage in cattle feed reduces the required amount of high-quality feedstuffs and thus reduces the competition for livestock feed and food for humans. (Flachowsky et al., 2017; Windisch & Flachowsky, 2020)

Increasing the amount of roughage in cattle nutrition contributes to rumen health and thus promotes animal welfare (Suárez et al., 2007; Chibisa et al., 2020). However, roughage-rich rations provide lower amounts of energy and nutrients. Furthermore, climate change and regional differences in arable farming conditions can influence forage production and quality (Trnka et al., 2004; Li et al., 2009; Lee et al., 2017). Therefore, investigating the lower nutrient and energy limits in cattle feeding is necessary. Modern livestock must be efficient in exploiting nutrients and energy in the offered feed and resilient to periods of low energy and nutrient intake to fulfill their performance potential. This research has demonstrated that Fleckvieh bulls are efficient and robust. Feeding high-energy rations led to significantly greater daily weight gains among animals in the 200–600 kg weight range (Table 3.3) and thus considerably shortened the fattening period in 780 kg HE-fed bulls (Table 3.4). The reduced fattening period demonstrates the high-energy fattening system’s economic efficiency.

Regarding physiological efficiency, bulls fed low-energy rations needed more time to reach the highest target weight (Table 3.4). However, low-energy rations did not adversely affect body composition or energy and nutrient content per kg of empty-body gain (Chapter 4.3). Accordingly, feeding high-energy rations is unnecessary from a metabolic point of view.

Fleckvieh bulls will need more time to grow when forage quality is negatively affected by regional or climatic conditions. However, the body composition at a particular live weight will not change. This observation leads to the assumption that the growth pattern of Fleckvieh bulls is genetically predefined and, to a certain extent, independent of the energy and nutrient supply. Thus, Fleckvieh bulls are resilient to variations in feed energy concentrations and can be fattened using roughage-rich diets, which positively affects animal welfare.

It should be noted that the rations used in this trial (Tables 3.1 & 3.2) contained a metabolizable protein to energy ratio within a range that allowed the bulls to show an adaptive response and thus maintain normal physiological growth. The protein to energy ratio needed to maintain normal physiological growth processes depends on the stage of relative maturity and changes due to allometric growth processes. While protein accretion decreases during cattle growth, fat accretion increases and is associated with enhanced energy accretion rates (Table 4.3). Consequently, the metabolizable protein to energy ratio required for cattle feed decreases as the animals' live weight increases, which should be considered in cattle feeding concepts (Chapter 4.4). Phase feeding growing cattle offers an excellent opportunity to provide animal feed that closely matches protein requirements and thus reduces nitrogen excretions that arise from protein oversupply.

An optimized protein to energy ratio in cattle feeding only ensures normal growth processes when it is based on an adequate protein supply. Changes in body tissue composition are expected when cattle face protein or energy undersupply or oversupply. In this research, bulls fed high-energy rations did not show increased fat accretion or body fat content (Chapter 4.3). Hence, the high-energy rations did not exceed the upper limit of energy supply, in which increased fat accretion is expected. These findings suggest that the Fleckvieh bull's maximum performance potential was not exploited by the amount of protein and energy provided in the high-energy TMR (Chapter 4.4).

Previous research into growing Fleckvieh bulls showed that feed restriction could reduce fattening performance (Schwarz et al., 1992) and fat accretion (Kirchgessner et al., 1994) in Fleckvieh bulls. As a result, the carcasses of bulls under restricted feeding conditions showed larger proportions of muscle and lower proportions of fat tissue than those of *ad libitum* fed bulls (Augustini et al., 1992). Additional research into reduced energy and nutrient supply under restricted feeding conditions similarly reported inferior fattening and slaughter performance in insufficiently fed cattle (Keogh et al., 2015; Manni et al., 2017). A similar effect can be achieved by reducing the amount of crude protein in cattle diets.

Inhuber et al. (2021) showed that reducing dietary crude protein in rations with equal energy content led to decreased DM and ME intake in growing Fleckvieh bulls. Consequently, bulls fed low crude protein diets showed lower daily weight gains, lower dressing percentages and tend to show inferior carcass classifications and carcass fat class scores (Inhuber et al., 2021). The studies show that a shortfall in protein or energy supply causes growth degradation and delays allometric growth processes in cattle.

Further studies are needed to investigate the lower limits of protein and energy supply and thus determine an ideal metabolizable protein to energy ratio that suits the different cattle growth stages. The studies should first determine the lower limit of protein supply and thus minimize cattle nitrogen excretion. Based on the lower limit of protein supply, further studies should investigate the lower limit of energy supply and, therefore, the upper limit of roughage feeding.

It can be concluded that cattle feeding recommendations should be regularly adjusted to meet the animals' physiological needs. Future feeding concepts should improve resource efficiency by reducing competition for food resources. Furthermore, phase feeding can reduce the negative environmental impacts of cattle excretions. Hence, sustainable cattle feeding concepts can contribute to resource conservation, environmental protection, and animal welfare.

6 Conclusions and outlook

This research aimed to generate basic data to determine the nutrient and energy requirements of growing Fleckvieh beef bulls under different feeding conditions. Therefore, analyses of body composition, nutrient, and energy accretion rates, and allometric growth patterns in Fleckvieh bulls fed rations with varying energy concentrations were performed.

An important step in generating basic data for determining the nutrient and energy requirements of growing Fleckvieh bulls was to calculate the energy and nutrient accretion rates in the animals. A third-order polynomial regression of live weight was used in this study to determine the composition of body tissues and nutrients in Fleckvieh bulls with live weights ranging from 100–800 kg. The first derivatives of the body-composition functions characterized expected gains in body tissues and nutrients at a given live weight. The same approach can also be used to calculate the accretion rates of individual minerals and amino acids in growing animals. Moreover, modeling the gain composition provided the opportunity to demonstrate typical allometric growth patterns in body tissues and nutrients in growing cattle.

Live mass gain in cattle was characterized by the unequal growth and development of individual body tissues. The results clearly illustrated allometric growth patterns comprising changes in tissue chemical composition, leading to changes in the bulls’ overall body chemical composition. Comparison with previous studies of bulls of the same breed and sex indicates that the empty-body tissue composition in current and former *ad libitum* fed Fleckvieh bulls with defined live weights has not changed in past decades. Furthermore, the Fleckvieh bulls’ body composition was not changed by feeding rations with different energy concentrations. These findings suggest that body composition within cattle breeds and sex depends on live weight or relative maturity rather than age. Furthermore, the results demonstrate that the growth patterns of Fleckvieh bulls are genetically predefined and, to a certain extent, independent of the energy and nutrient supply.

Fleckvieh bulls at the current genetic level efficiently exploited the energy and nutrients in the offered feed, which resulted in increased fattening performance and final weights, compared to Fleckvieh bulls in previous decades. Regarding the feed intake groups, bulls fed a high-energy diet exhibited increased growth performance during particular stages of the fattening period and thus superior economic efficiency. Increased daily weight gains in high-energy fed bulls were associated with higher daily energy and nutrient accretion rates. However, high-energy feeding did not change the energy and nutrient contents per kilogram of empty-body weight gain. Nonetheless, the composition of body weight gain in growing Fleckvieh bulls has changed during the past decades. Current Fleckvieh bulls with high live weights showed lower rates of crude protein accretion but higher rates of crude fat and energy accretion than bulls in previous decades. Therefore, phase feeding should be applied to feed cattle according to their physiological needs and thus reduce nitrogen excretions due to protein oversupply.

In terms of physiological efficiency, Fleckvieh bulls fed low-energy rations needed more time to reach the highest target weight. However, feeding low-energy rations did not adversely affect the body composition, carcass composition, or meat quality traits of growing Fleckvieh bulls. Accordingly, feeding high-energy rations is not necessary from a metabolic standpoint. Fleckvieh bulls can be fattened with lower energy and therefore roughage-rich rations due to their physiological advantages as ruminants, which contributes to resource efficiency and animal welfare.

In the future, feeding concepts should reduce competition for food resources and minimize the negative environmental impacts of cattle feeding. Hence, further studies of this type are required to evaluate the feeding recommendations for growing steers and heifers. Such studies should aim to determine the lower limits of metabolizable protein and energy in cattle feed, allowing normal physiological growth processes without compromising body tissue gain. Therefore, the studies should first investigate the lower limit of protein supply and, based on this, explore the lower limit of energy supply. Researchers should consider cattle growth processes and the resulting decline in the required protein to energy ratio in cattle feed. Phase feeding provides a useful tool for feeding the animals at the lower limit of their adaptable range throughout the growth process.

It can be concluded that recommendations for the energy and nutrient requirements of growing Fleckvieh bulls should be regularly adjusted to reflect enhanced growth potential and target weights as well as the animals’ energy and nutrient requirements. Future feeding concepts should aim to increase roughage in cattle nutrition to reduce competition for resources used in livestock feed and human food production. Combining roughage-rich rations and phase feeding improves resource efficiency and minimizes the negative environmental impacts of nitrogen excretions. In this way, sustainable cattle feeding concepts can contribute to resource conservation, environmental protection, and increased animal welfare.

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