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Histochemical composition of muscles differing in physiological function from three contrasting ruminant species

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Abstract

The utilisation of game meat contributes towards various Sustainable Development Goals; however, it is necessary to quantify and optimise game meat quality for the commercial market to ensure high and uniform product quality to ensure consumer satisfaction. Understanding the factors that impact game meat quality, like muscle fibre composition, can provide insight into the expected meat quality of certain game species and subsequently determine appropriate processing and cooking techniques. Therefore, the aim of the study was to compare the muscle fibre characteristics of two farmed game species and cattle. Cattle (*Bos Taurus*; n = 10), common eland (*Tragelaphus oryx*; n = 10), and fallow deer (*Dama dama*; n = 10) were slaughtered at approximately 18 months of age. The samples of the *longissimus thoracis et lumborum* (LTL), *triceps brachii* (TB), and *rectus abdominis* (RA) muscles were analysed for muscle fibre composition. Cattle muscles had larger cross-sectional areas for all muscle fibre types within all muscles compared to the common eland and fallow deer muscles. The LTL of the fallow deer and eland muscles showed lower proportions of type I and higher proportions of type IIA fibres than cattle. Moreover, the proportion of type I fibres was lower in the LTL of fallow deer and eland compared to other muscles, differences that were not observed in cattle. These results may be an important indicator of changes in muscle mass that could occur in these farmed species as a result of future breeding selection.

Keywords: cattle, common eland, fallow deer, *longissimus thoracis et lumborum*, muscle fibre, *rectus abdominis*, *triceps brachii*

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Introduction

As the human population continues to grow, food production will need to increase by at least 70% by 2050 (Crist *et al.*, 2017). This, along with the reality of climate change, will require increased livestock and crop production without losing more biodiversity or converting natural areas for cultivation (Crist *et al.*, 2017). The production of animal protein by domesticated ruminants is often criticised for its contribution to global warming and for excessive water consumption (Malan *et al.*, 2020; Tongwane & Moeletsi, 2020). Moreover, the rearing of traditional livestock for meat production is not efficient in some geographical areas due to various implications of climate change, including low-quality vegetation and drought conditions. One of the options to ensure sufficient production of animal protein is to use

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alternative meat sources, such as game animal species (Taylor *et al.*, 2020). In South Africa, game ranching is well-established and this method of farming of game species under natural conditions that are not suitable for growing agricultural crops or for intensive livestock breeding (marginal and dry areas) ensures more efficient utilisation of natural resources whilst contributing to biodiversity (Taylor *et al.*, 2021). Species that can be farm-raised under such conditions include various types of antelope and deer, which can be considered as alternative farming species due to their adaptability traits. One of the species that is known to thrive under drought conditions in comparison to traditional livestock, such as cattle, and that is more adaptable to heat stress, is the common eland (*Tragelaphus oryx*) (Watson & Owen-Smith, 2000). The eland is one of the largest antelope species, with a body size comparable to that of cattle. Although eland seems to achieve lower rates of body weight gains than domesticated species, their carcass yield is similar to some local cattle breeds from the same geographical origin (Needham *et al*., 2022). Moreover, eland has a higher tolerance to plant toxins and tannins, enabling them to utilise plants that would otherwise not be grazed by cattle (Flack, 2013).

One of the most commonly-farmed deer species worldwide is the fallow deer (*Dama dama*) (Kudrnáčová *et al.*, 2018). Fallow deer is a species of the *Cervidae* family, reaching a live weight of 40–100 kg in adult males, with good carcass yield and a high proportion of lean meat in the carcass (Volpelli *et al.*, 2002; Stanisz *et al.,* 2015; Kudrnáčová *et al.*, 2018). Although fallow deer are not native to South Africa, these cervids have adapted well to local conditions and their population has increased, yet they are currently underutilised. In light of growing interest in deer farms around the world, fallow deer could play a more important role as meat producers and contributors to food security in South Africa (Cawthorn *et al*., 2018). Fallow deer meat is a valuable source of protein and, in comparison with domesticated ruminants, has significantly lower amounts of intramuscular fat (Bureš *et al*., 2020).

Moreover, consumer awareness regarding animal husbandry and welfare is increasing, and thus venison and other game meat is an attractive alternative to meat produced under intensive production systems (Kudrnáčová *et al.*, 2018). Concurrently, consumer acceptance of game meat is increasing (Kempen *et al.,* 2023). This is primarily due to the perceived benefits of game/venison production, where animals are produced extensively on natural grazing (without feed additives or high-energy diets) and pharmaceuticals are seldom used; thus, game/venison is often deemed to be natural and organic (Kudrnáčová *et al.*, 2018). The challenges and opportunities of utilising wild game populations for meat production is discussed in the recent review of Needham *et al*. (2023), including the role that farmed game can play in improving the quality and safety of game meat. In addition to its nutritional value and perceived improved animal welfare, the organoleptic properties of game meat play an important role in consumer acceptance, and thus it is important to understand the factors that influence them. One of the most important properties of fresh meat, irrespective of species, is texture, which is influenced by numerous factors, including the muscle growth rate, muscle type, and muscle fibre composition and size (Lebedová *et al.*, 2022).

Understanding skeletal muscle growth and development is pivotal in the fields of animal and meat science (Rehfeldt *et al.*, 2004). Up to 60 % of the body weight of livestock is edible, and this is primarily muscle, consisting of muscle fibres (Lee *et al.*, 2010; Listrat *et al.*, 2016; Picard & Gagaoua, 2020). Muscle fibres can be considered as the functional metabolic unit of the muscle; variation in their composition allows for the wide variety of contraction types required by a functional body, but also affects changes in the muscle *post-mortem* (North & Hoffman, 2017). Their composition is thus one of the most important factors influencing physical and sensory meat quality parameters (Lefaucheur, 2010; Joo *et al.*, 2013). The histochemical composition of muscle fibres can be evaluated using several methods and has been described in a variety of muscles of various livestock and other animals (Lefaucheur, 2010; Joo *et al.*, 2013; Picard & Gagaoua, 2020). However, for some less common species or muscles, this description is still missing in current literature.

Although non/semi-domesticated species (like eland and fallow deer) have not yet undergone direct breeding selection for production traits, it can be expected that these farmed species may be subject to more intense selection in the future, which may lead to changes in the histological composition of their muscles as they become more “domesticated.” In contrast, cattle have been bred for these traits over a long time period during their domestication. Furthermore, understanding these muscle characteristics can provide insight into expected meat quality traits and guide appropriate processing and cooking techniques (Picard & Gagaoua, 2020). Therefore, the aim of the study was to compare the muscle fibre characteristics of muscles with different physiological and culinary purposes from fallow deer (a common cervid species for venison production), common eland (a popular antelope species for game meat production and hunting purposes), with dual-purpose Fleckvieh cattle.

Materials and Methods

All experimental procedures were conducted in accordance with Council Directive 86/609/EEC, concerning the protection of animals used for experimental and other scientific purposes, and were approved by the Animal Care Committees of the Institute of Animal Science (IAS) and the Czech University of Life Sciences (CZU), Prague (Permit: CZU 20/19).

A total of 30 carcasses from males of three different ruminant species were used: cattle (*Bos taurus*), common eland (*Tragelaphus oryx*), and fallow deer (*Dama dama*) that were slaughtered at approximately 18 months of age. The ten Fleckvieh (Simmental type dual-purpose breed) bulls were group-housed on straw bedded pens at the experimental unit of IAS Prague (50.0315350N, 14.6044803E) from approximately nine months of age. They were fed maize silage, legume silage, and lucerne hay with the addition of concentrates and mineral supplements. Cattle bulls were transported (2 km) to the abattoir when they reached slaughter age. They were stunned using captive bolt and exsanguinated (Lebedová *et al.*, 2022). Ten eland bulls were selected from the Czech University of Life Sciences Prague Common Eland Research Facilities (50.1283722N, 13.9580911E) according to their average age as determined by birth date records and were fed a similar cattle-type diet consisting of silage, a high-protein pelleted ration, and vitamin–mineral supplement (Needham *et al.*, 2020). Further details regarding the origin of the herd and their husbandry can be found in Bartoň *et al.* (2014), Needham *et al.* (2020), and Musa *et al.* (2021). They were slaughtered on-site at the research facilities, using captive bolt stunning, and transported to the same abattoir for processing, following the same procedures as Needham *et al.* (2020). Ten fallow deer males were randomly selected from a group of 45 animals born during the same calving season at a private deer farm at Mnich (49.1671744N, 14.9007092E), South Bohemian region, Czech Republic. The deer were kept together since weaning and then (at approximately 9 months of age) separated into three 2-ha paddocks with extensive grazing pasture (Kudrnáčová *et al.*, 2019).

During winter, the animals received haylage to compensate for the lack of pasture and received a mineral mixture. Fallow deer were also slaughtered on-farm using similar equipment and procedures as mentioned above for eland, and the carcasses were then transported (~22 km; ~25 min duration) to a small private abattoir at Soběslav, South Bohemia, for further processing. The slaughter and hot carcass weights of all animals were recorded.

Approximately 8 h *post mortem*, portions (5 × 3 × 3 cm) from the *longissimus thoracis et lumborum* (LTL, at the 9th–10th rib), *triceps brachii* (TB), and *rectus abdominis* (RA) muscles of each of the carcasses (right side) were removed. The sampling of the TB and RA muscles is described by Oury *et al.* (2010). Immediately after collection, the samples were cut into approximately 0.5 × 0.5 × 2 cm pieces, promptly frozen in isopentane chilled with liquid nitrogen, and transported to the laboratory, where they were kept at −80 °C until further analysis. For each muscle sample, 10-µm thick, serial transverse sections were cut from the frozen samples using a cryostat CM1850 (Leica Microsystems GmbH, Nussloch, Germany) set at −22 °C. These sections were then mounted onto glass slides and stained according to the method of Brooke & Kaiser (1970) to determine adenosine triphosphatase (ATPase) activity (pre-incubation in pH 10.3 or 4.3). Images were obtained using an optical microscope (Nikon Eclipse E200, Nikon, Tokyo, Japan; Figure 1). NIS-Elements AR 3.2. (Nikon Instruments Europe B.V., Amsterdam, Netherlands) was used to determine a number of parameters. First, the muscle fibres were classified into types I, IIA, and IIB (Brooke & Kaiser, 1970). Then, the following parameters were determined: mean cross-sectional area (CSA; µm^2) of the fibres, CSA of individual fibre types, fibre type proportion (ratio of the individual fibre type number from the total measured fibres), and relative area of fibres (ratio of the individual fibre type area of the total measured area). These analyses were performed on randomly selected serial sections of samples, and muscle bundles were taken into consideration. Approximately 250–400 fibres per sample were included in the analyses (Lebedová *et al*., 2022).

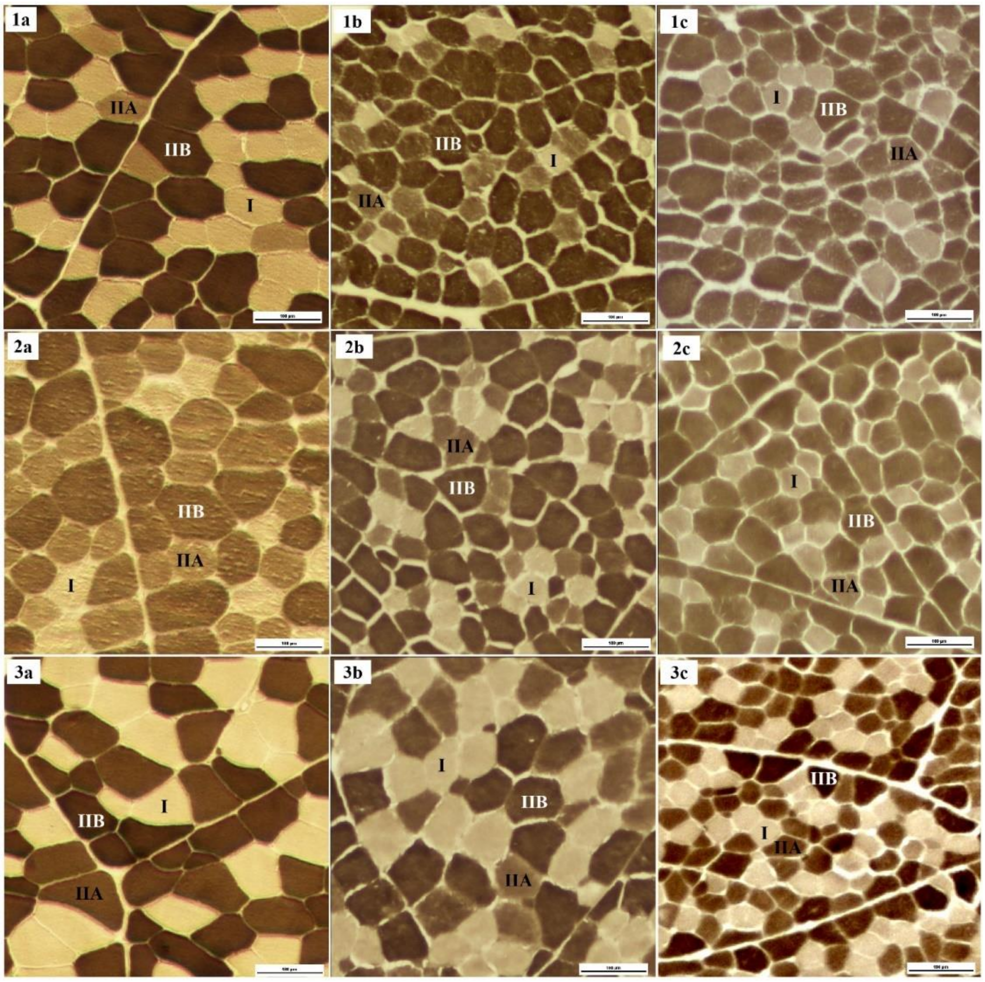

Figure 1 Muscle fibres, stained using myosin ATPase after alkaline pre-incubation, from cattle (*Bos Taurus*; a), common eland (*Tragelaphus oryx*; b) and fallow deer (*Dama dama*; c) *longissimus thoracis et lumborum* (1), *triceps brachii* (2) and *rectus abdominis* (3) muscles. Bar = 100 μm; I: fibre type I; IIA: fibre type IIA; IIB: fibre type IIB

Statistical analyses were performed using the statistical package SAS (Version 9.4, SAS Institute Inc., Cary, NC, USA). A mixed linear model (MIXED procedure and REML estimation method) was used, with animal species included as a fixed effect (Table 1). The data in Table 2 were analysed with inclusion of the fixed effect of species, muscle, and their interaction, and the random effect of animal. Data in Table 2 were calculated as least square means (LSM) of the simple effect of slices (by species and by muscle) and multiple comparisons were made with *P*-values adjusted using Tukey's range test (Lebedová *et al*., 2021). Differences were considered significant at 5 % ($P < 0.05$).

Results and Discussion

Table 1 depicts the slaughter parameters of the three different animal species slaughtered at a similar age (18 months). The heaviest slaughter and carcass weights were those of the cattle, followed by the eland, and the lightest were the fallow deer, which also had a lower dressing percentage than the other two species.

Table 1 Least square means for the slaughter parameters of three different animal species at approximately 18 months of age

	Cattle (*Bos taurus*)	Eland (*Tragelaphus oryx*)	Fallow deer (*Dama dama*)	SEM	*P*-value
Final live weight (kg)	680.2^{A}	271.3^{B}	44.9^{C}	11.90	<0.001
Hot carcass weight (kg)	384.0^{A}	150.3^{B}	22.8^{C}	7.78	<0.001
Dressing percentage	56.4^{A}	55.5^{A}	50.8^{B}	0.60	<0.001

SEM: Standard error of the mean
^{ABC} Values with different superscript in the same row differ (P <0.001)

Body size and weight of the animals derived from the studied species are known to be different; the final live and carcass weights of the individual species in this study correspond to the results of other studies performed on these species of comparable age (Volpelli *et al.*, 2002; Bureš & Bartoň, 2012, 2018; Kudrnáčová *et al.*, 2019; Needham *et al.*, 2019). Despite very different body weights, these species achieved similar carcass yields (i.e., dressing percentages). The eland in the current study showed dressing percentages comparable to dual-purpose or early maturing beef breeds (Bureš & Bartoň, 2018) rather than dairy breeds, as previously reported (Kotrba *et al.*, 2016). Lower dressing percentages found in the fallow deer correspond to the results found by Kudrnáčová *et al.* (2019) for fallow deer fed on pasture. However, when fallow deer receive supplementary feed (Kudrnáčová *et al.*, 2019), their dressing percentages are similar to the results reported in the current study for eland and cattle. Poor pasture conditions caused by a dry season likely impacted the dressing percentages for fallow deer in the current study.

Muscle fibre properties are influenced by several factors other than the animal species; these include the muscle location, breed, genotype, or sex, and also external factors, such as nutrition or physical activity (Joo *et al.*, 2013; Picard & Gagaoua, 2020). The resulting composition of muscle fibres, together with the formation of other tissues, affects the final meat quality of the muscle. The LTL, TB, and RA muscle histological composition of the three different ruminant species is presented in Table 2.

The largest CSAs of all fibre types were observed in cattle, whereas the smallest mean CSA and CSA of type IIB fibres were found in fallow deer LTL and RA muscles. Differences in the muscle mass of animals are related to muscle fibre number and size (Rehfeldt *et al.*, 2004). Although the carcass of dual-purpose cattle were approximately 15 times heavier than the fallow deer carcasses in the present study, the average muscle fibre CSA of the cattle muscles was only 2.5–3 times larger than that of the fallow deer. Similarly, eland carcasses were approximately six times heavier than those of the fallow deer, but the CSA of their muscle fibres was only one and a half times larger, or even comparable in the case of the TB muscle. This further supports the hypothesis that species-specific differences in muscle mass are primarily due to differences in the total number of muscle fibres (Rehfeldt *et al.*, 2004; Zochowska-Kujawska *et al.*, 2009; Lefaucheur, 2010), which is a parameter that is difficult to assess objectively in such large muscles.

Compared to other species, the cattle LTL had a higher proportion of type I and a lower proportion of type IIA fibres. The relative area of type I fibres was higher in cattle, whereas fallow deer had the highest relative area of type IIA fibres (the lowest was reported for cattle). Eland LTL muscles had a higher relative area of type IIB compared to the LTL of cattle. The proportion and relative area of type I fibres of TB muscle were lower in fallow deer than in cattle and eland muscles. Cattle and eland muscles also differed in their proportion of type IIA fibres, which was lower in the muscles from cattle TB, whereas the fallow deer TB had a higher proportion and relative area of type IIB fibres, compared to the eland. The RA muscle of the fallow deer showed a higher proportion of type I fibres compared to the other two species. The eland RA muscles had a lower relative area of type I fibres than cattle and fallow deer, and a higher relative area of type IIB fibres than the RA of cattle. Furthermore, the relative area of type IIA fibres was higher in cattle RA muscles than in fallow deer and eland RA muscles. The LTL muscle is widely used in studies assessing meat quality parameters due to its size and economic value.

Table 2 Least square means for the muscle fibre parameters of the *longissimus thoracis et lumborum* (LTL), *triceps brachii* (TB), and *rectus abdominis* (RA) muscle of three different animal species

		Cattle (*Bos taurus*)	Eland (*Tragelaphus oryx)*	Fallow deer (*Dama dama*)	SEM	*P*-value
		Cross-sectional area of fibres (µm²)				
Mean	LTL	3480^{Ay}	2098^{Bx}	1205^{C}	123.9	<0.001
	TB	3533^{Ay}	1626^{By}	1422^{B}	135.1	<0.001
	RA	3981^{Ax}	1966^{Bxy}	1298^{C}	185.2	<0.001
	P-value	0.004	0.012	0.391		
Type I	LTL	2704^{Ay}	1014^{B}	747^{B}	118.9	<0.001
	TB	2330^{Ay}	1041^{B}	843^{B}	89.8	<0.001
	RA	4006^{Ax}	1442^{B}	1099^{B}	224.8	<0.001
	P-value	<0.001	0.059	0.146		
Type IIA	LTL	3063^{Ay}	1275^{By}	976^{B}	128.7	<0.001
	TB	2883^{Ay}	1053^{By}	1080^{B}	126.3	<0.001
	RA	4398^{Ax}	1726^{Bx}	1154^{B}	164.3	<0.001
	P-value	<0.001	<0.001	0.529		
Type IIB	LTL	3923^{A}	2553^{B}	1345^{C}	166.9	<0.001
	TB	4233^{A}	2166^{B}	1655^{B}	206.4	<0.001
	RA	3835^{A}	2361^{B}	1514^{C}	219.3	<0.001
	P-value	0.138	0.183	0.332		
		Fibre type proportion (%)				
Type I	LTL	31.9^{Ax}	9.2^{By}	7.3^{Bz}	1.82	<0.001
	TB	25.0^{Ay}	24.1^{Ax}	13.9^{By}	2.34	<0.001
	RA	28.7^{Bxy}	27.5^{Bx}	35.8^{Ax}	1.83	0.011
	P-value	0.029	<0.001	<0.001		
Type IIA	LTL	7.8^{Bz}	24.3^{A}	27.1^{Ax}	1.63	<0.001
	TB	16.0^{By}	23.2^{A}	19.5^{ABy}	1.40	0.018
	RA	23.1^{x}	21.3	18.6^{y}	2.08	0.187
	P-value	<0.001	0.415	0.001		
Type IIB	LTL	60.3^{x}	66.5^{x}	65.7^{x}	2.28	0.168
	TB	59.0^{ABx}	52.7^{By}	66.6^{Ax}	2.73	0.001
	RA	48.2^{y}	51.2^{y}	45.6^{y}	2.36	0.288
	P-value	<0.001	<0.001	<0.001		
		Fibre relative area (%)				
Type I	LTL	25.3^{Ax}	4.4^{By}	4.5^{By}	1.91	<0.001
	TB	16.6^{Ay}	16.4^{Ax}	8.4^{By}	1.80	0.003
	RA	28.2^{Ax}	20.2^{Bx}	30.7^{Ax}	1.67	<0.001
	P-value	<0.001	<0.001	<0.001		
Type IIA	LTL	7.0^{Cz}	15.2^{B}	22.3^{Ax}	1.78	<0.001
	TB	13.1^{y}	15.5	14.6^{y}	1.32	0.629
	RA	25.6^{Ax}	19.0^{B}	16.5^{By}	2.15	0.002
	P-value	<0.001	0.198	0.005		
Type IIB	LTL	67.7^{Bx}	80.4^{Ax}	73.2^{ABx}	2.33	0.002
	TB	70.3^{ABx}	68.1^{By}	77.0^{Ax}	2.43	0.032
	RA	46.2^{By}	60.7^{Ay}	52.8^{ABy}	2.43	<0.001
	P-value	<0.001	<0.001	<0.001		

SEM: Standard error of the mean

^{ABC} Values with different superscript in the same row differ between species ($P < 0.05$)

^{xyz} Values with different superscript in the same column differ between muscles within the muscle fibre type ($P < 0.05$)

The muscle fibre characteristics of cattle LTL muscles have been extensively studied (Hwang *et al.*, 2010; Joo *et al.,* 2017; Listrat *et al.*, 2020; Lebedová *et al.*, 2021). The histological composition of cattle TB and/or RA muscle is described by Brandstetter *et al.* (1998), Kirchofer *et al.* (2002), Micol *et al.* (2009), Oury *et al.* (2009, 2010), Joo *et al.* (2017), Listrat *et al.* (2020), and Lebedová *et al.* (2022), and as demonstrated by these studies, their compositions are influenced by breed, sex, age, and the classification method or sampling location used for the analysis. In contrast to cattle, there is currently little information available regarding the fibre type composition of fallow deer and eland muscles, or any other deer and antelope species in fact, and those available sources have most often only evaluated the composition of the LTL muscle.

Muscle functionality largely determines muscle fibre composition, and in general, postural muscles are more oxidative and contain more type I fibres than those muscles involved in rapid muscle activity (Joo *et al.*, 2013; Picard and Gagaoua, 2020). From previous reports on muscle histological composition, the LTL is considered as a “white” muscle, the TB as an intermediate type, and the RA as a “red” oxidative muscle (Kirchofer *et al.*, 2002; Oury *et al.*, 2009). Differences in the histological parameters of the muscle fibres between individual muscles within an animal species are presented in the columns of Table 2. Cattle RA muscles had larger mean CSAs than their LTL and TB muscles, whereas in eland, the LTL had larger mean CSA than their TB muscle. The CSA of IIB fibres did not differ between the muscles of all species, whereas the CSA of IIA fibres was substantially larger in the RA than in the LTL and TB muscles of both the cattle and eland. The CSA of type I fibres of the RA muscle was also larger than in the LTL and TB muscle of cattle, and a similar trend (P = 0.059) was observed in eland. Similarly, other studies performed on cattle (Oury *et al.*, 2010; Joo *et al.*, 2017; Lebedová *et al.*, 2022) reported that the RA muscle tends to have a higher CSA of red fibres (I and IIA) than the LTL and TB muscles. Furthermore, the RA muscle is specific in some fibre characteristics that are typically opposite for other muscles, where red fibres have a higher CSA than the white fibre type IIB (Picard & Gagaoua, 2020). However, this trend was not observed in the RA of eland and fallow deer in the current study; comparison with other studies is difficult because there is a lack of information available on the histological composition of the RA muscle in other livestock besides cattle. The cattle LTL had a higher proportion of type I fibres than the TB muscle, whereas the proportion of type IIA was the highest in the RA muscle, and the lowest in the LTL muscle. The proportion of IIB fibres was the lowest in the RA muscle. The eland LTL had a higher proportion of IIB and a lower proportion of type I fibres than their TB and RA muscles. Similar to cattle, the fallow deer RA muscle had the lowest proportion of type IIB fibres. However, the proportion of type IIA fibres was higher in the LTL than in the TB and RA muscles, and the proportion of type I was the highest in the RA and the lowest in the LTL muscles of fallow deer. The TB muscle of cattle showed a lower relative area of type I than their LTL and RA; the relative area of IIA fibres was the highest in RA and the lowest in their LTL muscle. The RA muscle of cattle also had a lower relative area of IIB fibres than the TB and LTL. However, the eland LTL showed a lower relative area of type I and higher relative area of type IIB fibres than their TB and RA muscles. The RA of fallow deer had a higher relative area of type I and lower relative area of type IIB fibres. Moreover their LTL showed a higher relative area of type IIA than their TB and RA.

In the present study, significant interspecies differences were found in the proportion of different fibre types and their relative area within the LTL muscle, where eland and fallow deer had much lower proportions of type I fibres and higher proportions of type IIA than cattle. Similar results were found by Curry *et al.* (2012), who studied the muscle fibre traits of the *longissimus lumborum* and *vastus lateralis* muscles from fallow deer and springbok (*Antidorcas marsupialis*), using histochemical and immunohistochemistry analyses. They demonstrated that fallow deer had a substantially higher proportion of IIA and a lower proportion of IIX (IIB) fibres compared to springbok. North and Hoffman (2017) further investigated the fibre-type composition of springbok muscles and found an even lower proportion of type I fibres (2.4 %) in the LTL. The histological composition of the *longissimus lumborum* and *biceps femoris* muscles of fallow deer were evaluated by Salomon *et al.* (1992), who classified the fibres using a combination of NADH-TR and ATPase staining into STO (slow-twitch oxidative), FTO (fast-twitch oxidative), and FTG (fast-twitch glycolytic). The *longissimus* muscle had a relative proportion of STO (I) fibres of 4.6–12.3%, depending on the age of the animals, whereas the proportion of FTO (IIA) was very high (62–71.7%). Zochowska-Kujawska *et al.* (2009) compared the muscle fibre traits of the *semimembranosus* muscle from fallow deer and three other game species – wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*). Fallow deer had a lower percentage of type IIA (9.4 %) than all other species (22–31 %), a higher percentage of type I fibres than roe deer, and a higher percentage of IIB fibres (60.5 %) than red deer (42.4 %) and wild boars (37 %).

In their other study, Zochowska-Kujawska *et al.* (2007) considered a wider range of roe deer muscles, including the *longissimus*, *biceps femoris,* and *semimembranosus* muscles. A lower proportion of type I fibres was reported within the *longissimus* muscle compared to the other muscles, as similarly found in eland and fallow deer in the present study. The muscle fibre traits of the *longissimus* muscle from four Southern African wild ruminants were studied by Kohn *et al.* (2007) in blesbok (*Damaliscus dorcas phillipsi*), kudu (*Tragelaphus strepsiceros*), black wildebeest (*Connochaetes gnou*), and blue wildebeest (*Connochaetes taurinus*). All four species' muscles contained a relatively high percentage of IIX fibres and low percentage (under 15 %) of fibre type I, which was similar for eland and fallow deer in the present study, as well as in the study of Curry *et al.* (2012). This finding seems to be a recurring observation for these types of wild animals, likely indicating a predominant genetic component affecting muscle fibre type (Kohn *et al.*, 2007, 2011; Curry *et al.*, 2012). Although muscles with different functions were studied by Curry *et al.* (2012), no differences in the relative fibre type distribution were found between the *vastus lateralis* and *longissimus lumborum* from fallow deer and springbok, whereas differences between these two muscles were reported for black wildebeest (Kohn *et al.*, 2011). This could support the statement that not all game species are the same, and with the exception of muscle location and function, there is a great genetic contribution towards fibre type distribution within muscle groups (Curry *et al.*, 2012). Moreover, fibre type can change as a result of external factors, including physical activity and environment (Kohn *et al.*, 2007; Lefaucheur, 2010). Antelope and deer have the ability to run at great speeds and are good jumpers, and thus it could be necessary for the LTL muscle to have a high proportion of type IIX/IIB fibres to generate the appropriate force for jumping (Kohn *et al.*, 2007). However, in the present study, the animals were kept in farmed conditions, in which their physical activity and behaviour (i.e., no predators/treats, continuous access to food) is different compared to wild individuals. Despite their captive farming conditions, the common eland and fallow deer have not been intensively and decisively selected for rapid growth rate and meat quality traits. Further research is needed to determine the effect of environmental factors, animal husbandry, and breeding selection on these muscle characteristics, and their impact on meat quality parameters.

Conclusions

There was a high variability in the muscle fibre composition between the evaluated species and between the muscles, despite the animals being of the same sex and slaughtered at similar ages. Both studied game species (common eland and fallow deer) showed lower CSAs of all muscle fibre types within all evaluated muscles compared to Fleckvieh cattle. Moreover, the LTL of cattle had a higher proportion and relative area of type I fibres, and lower proportion and relative area of type IIA fibres than the LTL of eland and fallow deer.

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Authors' contributions

N.L.: investigation, visualisation, writing – original draft. D.B.: conceptualization, methodology, investigation, formal analysis, writing – original draft. T.N.: investigation, validation, writing – original draft. L.B.: conceptualization, methodology, investigation, writing – review and editing, funding acquisition. L.C.H.: validation, writing – review and editing.

Conflict of interest declaration

There is no conflict of interest to declare.

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