frontiers | Frontiers in Animal Science

TYPE Original Research
PUBLISHED 03 October 2025
DOI 10.3389/fanim.2025.1656623

OPEN ACCESS

EDITED BY
George Attard,
University of Malta, Malta

REVIEWED BY
Simara Larissa Fanalli,
University of São Paulo, Brazil
Marek Babicz,
University of Life Sciences in Lublin, Poland

*CORRESPONDENCE
Simona Tarricone
simona.tarricone@uniba.it

RECEIVED 30 June 2025
ACCEPTED 17 September 2025
PUBLISHED 03 October 2025

CITATION
Karatosidi D, Symeon G, Michailidis G, Avgeris E, Tarricone S, Giannico F and Colonna MA (2025) Meat quality in autochthonous Mediterranean pig breeds reared in organic production systems. *Front. Anim. Sci.* 6:1656623. doi: 10.3389/fanim.2025.1656623

Meat quality in autochthonous Mediterranean pig breeds reared in organic production systems

Despoina Karatosidi[1], Georgios Symeon[1], Georgios Michailidis[2], Efthymios Avgeris[3], Simona Tarricone[4]*, Francesco Giannico[5] and Maria Antonietta Colonna[4]

[1]Research Institute of Animal Science, Hellenic Agricultural Organization-DIMITRA, Giannitsa, Greece, [2]Department of Animal Production, Aristotle University of Thessaloniki/School of Agriculture, Thessaloniki, Greece, [3]Panellinia Enosi Ektropheon Autochthonon Fylon Agrotikon Zoon – PEEAAFAZ, Trikala, Greece, [4]Department of Soil, Plant and Food Science, University of Bari Aldo Moro, Bari, Italy, [5]Department of Veterinary Medicine, University of Bari Aldo Moro, Valenzano (BA), Italy

Black pig breeds are autochthonous populations present in many Mediterranean countries, reared on sustainable production systems as they can exploit the feed resources available on the territory. While in Italy the black pig breeds have been thoroughly studied, in Greece there is still lack of information about the productive performances of this animal. This is a comparative study aiming at investigating on the carcass traits and meat quality features of the autochthonous Greek Black Pig and Italian Apulo-Calabrese black pig reared under organic production systems, typical of the rural areas of the two countries, on the quality parameters, chemical composition and fatty acid profile of the *Longissisum lumborum* muscle. A total of 40 pigs were used, 20 for each genotype, within each genotype two sub-groups were made and slaughtered at 9 or 12 months of age, respectively. When slaughtered at 12 months of age, meat from the Greek pig was brighter and more tender than the Apulo-Calabrese, while the chemical composition from the Italian breed showed a lower protein and intramuscular fat content than the Greek one. A higher percentage of Saturated Fatty Acids (SFA), total n-3 and n-6 fatty acids in turn of a lower amount of Mono Unsaturated Fatty Acids (MUFA) was found in meat from both the Greek groups. This trial may be considered as a first step to evaluate meat characteristics of the autochthonous Greek black pig and, therefore, a tool to increase awareness of this local genotype and its exploitation.

KEYWORDS

pigs, autochthonous, sustainable rearing, meat quality, fatty acid profile

1 Introduction

Traditionally, pig grazing systems are a possible source of income from livestock in internal regions of the Mediterranean Basin (Food and Agriculture Organization of the United Nations, 2014a). This has led rural populations to preserve the historical and cultural heritage related to local animal breeds and avoid biodiversity loss. To date, there is a growing interest towards the

10.3389/fanim.2025.1656623

TABLE 1 Selection of autochthonous pig breeds in the Mediterranean zone*.

Italy	Spain	France	Greece
Apulo-Calabrese	Celta	Bayeux	Greek black
Bergamasca nera	Chato Murciano	Blanc de l'Ouest	
Casertana	Gochu Asturcelta	Carélie	
Cinta Senese	Ibérico	Corse	
Macchiaiola Maremmana	Ibérico (Dorado Gaditano)	Creole	
Mora Romagnola	Ibérico (Mamellado)	Gallia	
Napoletana Fulva	Ibérico (Negro Entrepelado)	Gasconne	
Nero dei Lepini	Ibérico (Negro Lampiño)	Pie Noir du Pays Basque	
Nero dei Monti Dauni Meridionali	Iberico (Retinto)	Porc de Saint Yriex	
Nero Reatino	Ibérico (Torbiscal)		
Nero Siciliano	Manchada de Jabugo		
Parmigiana Nera	Negra Canaria		
Pugliese	Negra Mallorquina		
Sarda			
Siciliano			
Suino dei Nebrodi e Madonie			

*Source: FAO Domestic Animal Diversity Information System (DAD-IS) (http://dad.fao.org/).

nutritional properties and high quality of pig products (Sarmiento-García and Vieira-Aller, 2023). Consumers are oriented to foods of animal origin that are perceived as being healthy (Bondoc, 2015; Goracci and Camilli, 2025). Pig-meat acceptability varies widely depending on cultural traditions, age, socioeconomic conditions, and family habits that influence the consumers' preference (Razmaitė et al., 2022; Sarmiento-García and Vieira-Aller, 2023). The EU Regulation N. 2018/848, concerning organic production, strongly suggests valorizing animal breeds characterized by longevity, vitality, ability to adapt to the environment, and disease resistance (European Parliament, 2018). Preference should be given to local breeds and genetic lines, privileging genetic diversity. Organic production performs a twofold social role, since it ensures the functioning of the organic products market while satisfying the consumer's demand for healthy food; at the same time, organic farming contributes to the protection of the environment, the preservation of flora and fauna in rural areas, and their dynamic and sustainable development (Golovina et al., 2025). The concept of integrated agroforestry and silvo-pastoral systems, based on connections between conventional agriculture with other on-farm services (e.g., tourism, educational activities, social agriculture, etc.) provides rural populations with the chance to diversify and increase incomes from their multifunctional farms involved in food production and environmental conservation. This system allows the integration of forests, tree plantations and herbaceous crops with grazing animals. Many aspects of meat production quality are related to genotype, sex, age of the animals and the breeding system.

The United Nations' Food and Agriculture Organization (FAO) in the Domestic Animal Diversity Information System (DAD-IS) reports some of the autochthonous Mediterranean pig breeds, as shown in Table 1. According to this database, many breeds still exist, while many others are suffering extinction or nearly so (http://dad.fao.org). Moreover, in each of these countries, only some of the breeds have a real chance of survival, primarily related to their final products endowed with high added value (Pugliese and Sirtori, 2012). In Spain, even though there are several autochthonous breeds, the Ibérico characterizes the Spanish pork market and represents the result of a strong cooperation between public institutions, producers, and scientists. In recent years, demand for Iberian pig products has increased, which is attributed to a revaluation of traditional, top-quality products (Ortiz et al., 2021). In France, the main autochthonous breeds such as the Blanc de l'Ouest, Porc Basque and Nustrale maintain their genetic variation within breeds and provide economic advantages through the production of high-quality products (Labroue et al., 2001). In Italy, only six pig breeds survived the transformations that occurred in agriculture in the last century, which are the Apulo-Calabrese, Casertana, Cinta Senese, Mora Romagnola, Nero Siciliano, and Sarda breeds. These genotypes have been recognized as preserved breeds and have a National Herdbook while others are declared extinct (Bittante, 2011). In Greece, there is only one autochthonous pig breed trying to expand after the 1980s (Antikas, 2003; Ribani et al., 2023).

The Greek Black Pig (also known as Greek Pig) dates to the ancient times but its genetic pool might have been shaped by many more recent events (Antikas, 2003). Greek black pigs are very similar to the black Mediterranean pigs, characterized by high

FIGURE 1
Greek black pigs on the left (source: authors' archive), Apulo-Calabrese on the right (source: Francesco Carriero).

rusticity and adaptability to environmental conditions and by substantial capacity to use local food resources (Michailidou et al., 2014). This breed was the only one raised in Greece until the 1960s and it represented one of the main traditional outdoor livestock production systems in Greece (Papatsiros et al., 2012). The relevance of this genotype, however, decreased with the advent of intensive pork production systems where cosmopolitan and genetically improved breeds and lines replaced this local breed.

Nowadays, small populations of Greek Black pigs are present throughout mainland Greece, for a total of approximately 3000 animals (http://dad.fao.org), mainly concentrated in the central and northern regions of the country.

The animals have usually solid black coat color, with medium-long hairs, slightly falling ears, and middle-sized snout (Figure 1).

Only 80% of piglets born reach slaughter age, due to exogenous factors such as carnivores and unfavorable environmental conditions. Usually, pigs are slaughtered at 6–12 months of age, to obtain a carcass of about 20–50 kg, but often they can be slaughtered when they reach a live weight of about 80–130 kg. The pigs are reared in a semi extensive farming system, based on mountain pastures where they are fed with acorns, except for the mating season, in which they are supplemented with concentrates (Papatsiros et al., 2012). Their body weight is closely related to the breeding system: pigs that live in hilly and inaccessible areas are smaller in contrast to those raised on grass pastures or farmed receiving supplementary feeding at housing.

The Apulo-Calabrese breed is a swine population that has been established over the centuries and spread with the transhumance of the flocks on the road routes dating back to Roman times (Tarricone et al., 2019). In the past century, black coat pigs, capable of using poor food resources, were present along the Apennine foothills. The abandonment of the lands and the uncontrolled introduction of cosmopolitan breeds provoked a rapid decline of the breed too, until, eventually in the 1990s, a recovery action started. The conservation program has progressively been consolidated, and the herd book was established in 2001 (Bozzi et al., 2019). Nowadays, Apulo-Calabrese pigs are raised in the southern regions of Italy, thanks to peasant farming systems which use agroforestry practices (Aboagye et al., 2020). The Italian Pig Breeders Association (ANAS) has the duty to control the breeds and their herdbooks in order to collect the data for selection programs and to promote and protect pig production (Figure 1) (ANAS, 2023, 2025).

Recently, the Apulian Black Pig District is being established with the aim of creating an effective tool for pig farms, by promoting dialogue with regional and national institutions in order to facilitate access to development, innovation, and sustainability opportunities in the black pig sector (Apulian Region, 2007). The District will involve breeders, processing companies, and institutions, and its goal is to ensure the quality and uniqueness of black pig products, as the result of traditional feeding and management practices (Apulian Region 2017; 2024). The district includes the geographical Apulian areas of Capitanata, Murgia, and Valle d'Itria, where pigs are raised on small farms that practice organic production of crops used also for animal feeding.

The valorization of this indigenous pig genotype by implementing tools to promote local entrepreneurship needs the characterization of the black pig production, in terms of productive performances and meat quality; the realization of the District may represent a virtuous model that may be transferred also to other countries, such as Greece.

The aim of this study was to compare meat production and quality from two local black pig breeds, one Italian and one Greek, reared in common organic production systems and slaughtered at two ages, 9 and 12 months, respectively. The carcass composition, physical properties, chemical and fatty acid composition of meat, in relation to the genotype and slaughtering age, were assessed.

2 Materials and methods

2.1 Animal management and feeding strategy

In collaboration with the Panhellenic Association of Autochthonous Farm Animal Breeders (PEEAFAZ) in Greece and the Italian National Association Pig Breeders (ANAS, Associazione Nazionale Allevatori Suini), we identified pig

TABLE 2 Reproductive traits of Apulo-Calabrese and Greek Pigs.

Reproductive traits	Apulo-Calabrese*	Greek Pig**
Age at reproductive maturity (months)	10 ± 0.50	10 ± 0.50
Weight at reproductive maturity (kg)	95 ± 5	85 ± 5
Age at first parturition (months)	13 ± 0.50	13 ± 0.50
Litter per year (N)	1.7 ± 0.25	1.8 ± 0.20
Prolificacy (N. piglets/litter)	7.05 ± 0.95	8.48 ± 1.94
Birth Live Weight (kg)	1.0 ± 0.20	1.0 ± 0.20
Duration of lactation (d)	50 ± 5	60 ± 7
Piglet Weaning Weight (kg)	6.75 ± 1.35	7.69 ± 0.69

*Bozzi et al., 2019; **Personal data.

breeding farms applying the same organic management practices and located at the same latitude. The Italian farm was allocated in a mountain area (750 m asl), where the mean annual temperature was 15.5 °C, with the highest mean temperature recorded in July (25.2 °C) and the mean total precipitation was 434 mm per year, with 13 snowy days during the months of December 2023 and January and February 2024, in which the mean temperatures were 7.1, 5.8 and 6.6 °C, respectively, according to the historic data recorded by the Italian Air Force (https://www.meteoam.it/it/home). The Greek counterpart farm was situated at 699 m asl; the mean annual temperature was 16.2 °C, in July the mean temperature was 27.5 °C, with a total precipitation of 462 mm per year and 9 snowy days in January and February 2024, when the mean temperature was 5.3 °C (https://www.meteoam.it/it/home).

All animal-related procedures complied with the Directive 2010/63/EU of the European Parliament (2010). A total of 80 male piglets were included in this study, 40 Greek Black pigs (GP) and 40 ApuloCalabrese pigs (AC), born from parents registered in the relevant herd books of each breed, during April-May 2023. All the pigs were reared according to the traditional farming system for the Greek Black and Apulo-Calabrese pig breeds, respectively. The piglets were exclusively milk-fed until they reached the age of about (60 ± 7 days; end of July). The reproductive traits of the ApuloCalabrese and Greek Pigs are shown in Table 2.

At weaning, within each breed, two batches of 20 piglets were made in relation to the age at slaughtering, that was 9 or 12 months. Ten litters from five boars were selected within each genotype; among each litter, 2 pairs of males were selected and divided into the two batches.

Within batches, pigs from one litter were allocated as equally as possible between the two slaughtering age groups, in order to have homogeneous groups for genealogy, age and live weight. The initial weight of the piglets was 35 ± 9 and 45 ± 7 kg, for GP and AC groups, respectively.

Piglets were housed in a loose barn for recovery during the evening and in adverse weather days while during the day they had free access to a fenced private pasture, grazing on a mixture of wheat (45%), barley (30%) and oat (25%) in both Greek and Italian locations, in order to minimize the feeding differences between the two environments. Both outdoors and indoors, pigs from each batch were kept loosely separated, in order to allow olfactory, auditory and some physical contacts among pigs, though maintaining distinct feeding.

Pigs were weighed individually at the start of the experiment, and monthly during the experimental period corresponding to the growing phase (until 80 ± 5 kg); afterwards they received the finisher feed until the age of slaughter. Pigs were observed daily during the experimental period to evaluate the pen and animal cleanliness, and overall wellness appearance of the animals.

2.1.1 Feeding strategy

During the day, the animals were kept outdoors and allowed to graze, as described above. At housing, they received *ad libitum* a grower or finisher pelleted feed in relation to the growing phase, along with the grassland hay. The pelleted feeds administered during the growing and finishing phases had the same ingredient and chemical composition in order to minimize feeding differences across countries. All pigs had free access to fresh water, that was always available indoors and outdoors.

The feed ingredients and the chemical composition of the pasture and the supplementary feed, as well as their fatty acid profile, are shown in Table 3.

2.2 Slaughter and sampling procedures

The animals were slaughtered at the age of 9 (N. = 40) and 12 (N. = 40) months, according to the EU legislation (Regulation EC No. 1099/2009) (European Parliament, 2009). After fasting for 12 h, with free access to water, pigs were transported to a local public slaughterhouse and weighed immediately before slaughtering (slaughter weight). After slaughtering, the hot carcass, skin and gastrointestinal tract were also weighed. Carcasses were hung and chilled at 0–4 °C (80–82% relative humidity) for 24 h and then re-weighed. The refrigerated carcasses were split into two halves across the mid-line, the right side was divided into different cuts, the meat cuts were stored at 4 °C for further 24 h and then the shoulder, loin and ham were dissected into their tissue components (lean, dissectible fat and bone), which were weighed. From each carcass, the 9–11th rib section of the *Longissimus lumborum* muscle was removed and transported from the slaughterhouse to the laboratory under refrigerated conditions.

TABLE 3 Feed ingredients (g/kg as fed basis), chemical (% dry matter basis) and FA composition (% FA methyl esters) of the supplementary diet.

Ingredient	Concentrate[1]		Grassland hay
	Grower	Finisher	
Corn meal	–	400.00	
Barley meal	300.00	250.00	
Dehulled sunflower meal	100.00	0.00	
Wheat flour shorts	200.00	150.00	
Faba beans	220.00	100.00	
Wheat middlings	150.00	100.00	
Limestone	12.00	12.00	
Monocalcium phospate	8.00	8.00	
Premix vitamins-minerals[2]	4.00	4.50	
Sodium chloride	4.00	4.00	
L-lysine	2.00	1.50	
Chemical composition (% on DM basis)			
Crude protein	18.25	15.14	10.72
Starch	32.50	47.60	–
Ether extract	3.44	2.94	1.37
Ash	3.45	2.72	9.58
Crude fiber	8.14	5.75	33.94
NDF[3]	–	–	60.38
ADF[4]	–	–	37.43
ADL[5]	–	–	9.31
DE, Mcal/kg	12.31	12.69	11.25
Fatty acids (% FA methyl esters)			
C16:0 (palmitic)	10.01	9.23	13.45
C18:0 (stearic)	1.32	1.18	3.03
C18:1 n-9, cis 9 (oleic)	19.03	17.78	12.13
C18:2 n-6 (linoleic)	14.81	15.16	31.00
C18:3 n-3 (α-linolenic)	3.99	4.65	2.57
C22:5 n-3 (DPA)	0.54	0.46	0.00
C22:6 n-3 (DHA)	0.37	0.29	0.01

[1]Grower: from the beginning of the feeding trial to 80 ± 5 kg; Finishing: from 80 ± 5 kg until slaughtering; [2]1 kg of Premix contains: vitamin A 6,000 IU, vitamin D3 800 IU, vitamin E 20 mg, niacin 6 mg, Ca D-pantothenate 4 mg, riboflavin 1.5 mg, vitamin K 1 mg, vitamin B6 1 mg, vitamin B1 0.8 mg, folic acid 0.25 mg, biotin 0.05 mg, vitamin B12 0.01 mg, choline Cl 600 mg, MnO 25.8 mg, ZnO 24.8 mg, $FeSO_4$· 2O 76 mg, $FeCO_3$· 2O 20.7 mg, $CuSO_4$· 22O 19.65 mg, $Ca(IO_3)2$ 0.62 mg, Na_2SeO_3 0.18 mg, L-lysine monohydrochloride 1.326 mg; [3]NDF, neutral detergent fiber; [4]ADF, acid detergent fiber; [5]ADL, acid detergent lignin.

2.3 Physical parameters of meat

The pH values were measured on two points of the *Longissimus lumborum* (Ll) muscle, 1 h after slaughter (pH_1) and after 24 h refrigeration (pH_{24}) using a portable instrument (Eutech Instruments XS PH110, Singapore, Singapore) with a Hamilton Double Pored penetrating electrode.

Meat color (L* = lightness, a* = redness, b* = yellowness) was determined using a Hunter Lab MiniscanTM XE Spectrophotometer (Model 4500/L, 45/0 LAV, 3.20 cm diameter aperture, 10 standard observer, focusing at 25 mm, illuminant D65/10, Hunter Associates Laboratory Inc., Reston, VA, USA). Three readings were taken for each sample by placing the instrument on different meat-handling surfaces. The instrument was normalized to a standard white tile before performing the analysis (Y = 92.8, x = 0.3162 and y = 0.3322). The reflectance measurements were performed after the samples were allowed to oxygenate in the air for at least 30 min to take stable measurements.

Homogeneous samples, approximately 5 cm thick, were cut from the *Longissimus lumborum* muscle and cooked in a ventilated electric oven at 165 °C until an internal temperature of 75 °C was reached in the center of the meat sample, as recorded by a thermocouple. To calculate the percentage of water loss during cooking, meat samples were weighed before and after cooking (Colonna et al., 2021). Raw and cooked Ll muscle samples (25.4 mm in diameter, with fibers perpendicular to the direction of the blade) were assessed for shear force (in triplicate) using a WB device, with a cutting speed of 200 mm/min and shearing until the sample was completely cut. The shear force value reported for each steak was the average value for all the evaluated cores.

The rest of the *Longissimus lumborum* muscle was homogenized in a blender and stored for 1 h at 4 °C until subsequent analysis for chemical composition and intra-muscular fatty acid profile.

2.4 Chemical composition and fatty acid analyses of meat

For the chemical composition of meat, AOAC procedures (2023) were used to assess the moisture, ether extract, protein, and ash.

Fat was extracted according to the method suggested by Folch et al. (1957), using a 2:1 chloroform/methanol (v/v) solution to determine the fatty acid profile. The fatty acids were then methylated using a KOH/methanol 2N solution (Christie, 1982) and analyzed with a gas chromatograph (Shimadzu GC-17A with FID detector, Kyoto, Japan) equipped with a flame ionization detector and fitted with a PBX-70 capillary column (60 m, 0.25 internal diameter and 0.25 μm film thickness, SGE) and using a split/splitless injection system (split ratio of 1:30) and helium as a carrier gas at a flow rate of 1.5 mL/min. The injection port and detector were maintained at 245 and 280 °C, respectively. The column oven temperature was programmed for 5 min at 135 °C,

TABLE 4 Live weights and dressing percentages of Apulo-Calabrese (AC) and Greek (GP) autochthonous pig breeds slaughtered at 9 and 12 months of age.

Items	AC		GP		SEM[1]	Effects[2]		
	9	12	9	12		B	SA	BxSA
Live weight (kg)	124.6[d]	138.2[c]	128.3[d]	138.1[c]	5.3	0.760	0.041	0.743
Right side carcass weight (kg)	49.4[d]	55.8[c]	47.5[d]	55.2[c]	2.9	0.712	0.021	0.726
Hot dressing (%)	82.1[A]	82.3[A]	76.2[B]	80.2[B]	1.3	0.003	0.148	0.187
Cold dressing (%)	74.4	79.4	74.2	79.4	1.5	0.112	0.064	0.089

[1]SEM, standard error of means. Differences between breed within each slaughtering age: A, B, $p < 0.01$. Differences between slaughtering ages within the breed: c, d: $p < 0.05$.

TABLE 5 Deboning of major cuts of Apulo-Calabrese (AC) and Greek (GP) autochthonous pig breeds slaughtered at 9 and 12 months of age.

Items	AC		GP		SEM[1]	Effects[2]		
	9	12	9	12		B	SA	BxSA
Shoulder								
Weight (kg)	8.9[D]	11.4[C]	8.8[D]	10.9[C]	0.3	0.487	0.001	0.668
% lean	74.9[C]	69.2[D]	75.7[C]	70.3[D]	0.8	0.235	0.001	0.877
% fat	5.6[c]	4.2[d]	5.2[c]	3.9[d]	0.5	0.525	0.011	0.867
% bone	7.7[D]	13.7[C]	7.5[D]	12.9[C]	0.9	0.555	0.001	0.766
% rind	11.8	12.9	11.6	12.9	0.9	0.366	0.092	0.367
Ham								
Weight (kg)	14.5	16.0	15.2	15.8	0.5	0.683	0.062	0.414
% lean	75.3[C]	71.2[D]	76.1[C]	72.3[D]	0.6	0.194	0.001	0.814
% fat	5.5	5.1	5.7	5.1	0.6	0.815	0.556	0.778
% bone	10.5[D]	13.4[C]	10.0[D]	12.7[C]	0.5	0.266	0.001	0.855
% rind	8.7	10.3	8.2	9.9	0.4	0.317	0.079	0.197
Loin								
Weight (kg)	8.0	8.7	8.4	8.5	0.5	0.844	0.547	0.559
% lean	60.1[c]	54.4[d]	59.4	56.6	1.6	0.755	0.014	0.367
% fat	7.2[d]	9.7[c]	7.8[d]	9.2[c]	0.9	0.789	0.035	0.567
% bone	19.4	20.5	19.6	20.0	1.2	0.745	0.578	0.878
% rind	13.3	15.4	13.2	14.2	0.8	0.367	0.355	0.689

[1]SEM, standard error of means. Differences between slaughtering ages within the breed: C, D: $p < 0.01$; c, d: $p < 0.05$.

followed by an increase of 3 °C/min to 210 °C, and finally held at 210 °C for 20 min. Fatty acids were identified by comparison of retention times to authentic standards for percentage area normalization. Fatty acids were expressed as a percentage (wt/wt) of total methylated fatty acids.

The food risk factors of meat were determined by calculating the atherogenic (AI) and thrombogenic (TI) indices (Ulbricht and Southgate, 1991):

$$AI = [(C12:0 + 4 \times C14:0 + C16:0)] \div [\Sigma MUFA + \Sigma n-6 + \Sigma n-3]$$

$$TI = [(C14:0 + C16:0 + C18:0)] \div [(0.5 \times \Sigma MUFA + 0.5 \times \Sigma n-6 + 3 \times \Sigma n-3 + \Sigma n-3)/\Sigma n-6]$$

where MUFA are monounsaturated fatty acids.

TABLE 6 Physical properties and chemical composition of *Longissimus Lumborum* muscle of Apulo-Calabrese (AC) and Greek (GP) autochthonous pig breeds slaughtered at 9 and 12 months of age.

Items	AC		GP		SEM[1]	Effects[2]		
	9	12	9	12		B	SA	BxSA
Physical properties								
pH	5.72	5.86	5.79	5.92	0.13	0.699	0.299	0.989
L*	55.23	56.39	55.87	56.78	0.96	0.655	0.266	0.844
a*	5.52^{D}	8.11^{C}	5.68^{D}	8.05^{C}	0.59	0.867	0.001	0.855
b*	12.83	13.33	12.92	13.62	0.29	0.556	0.058	0.631
WBS	2.91	3.53	3.23	3.73	0.37	0.578	0.147	0.877
Chemical composition								
Moisture (%)	$72.36^{b,d}$	$73.61^{b,c}$	$73.67^{a,d}$	$74.65^{a,c}$	0.37	0.036	0.026	0.788
Proteins (%)	22.06^{A}	21.33^{A}	19.41^{B}	18.86^{B}	0.38	0.001	0.091	0.899
Lipids (%)	$3.36^{B,c}$	$1.95^{B,d}$	$4.35^{A,c}$	$3.69^{A,d}$	0.44	0.008	0.039	0.423
Ash (%)	1.44^{A}	1.29	0.78^{B}	1.23	0.09	0.001	0.399	0.036
N-Free Extract (%)	$0.72^{b,d}$	1.82^{c}	$1.77^{a,c}$	1.61^{d}	0.22	0.044	0.023	0.047

[1]SEM, standard error of means. Differences between breed within each slaughtering age: A, B < 0.01; a, b, p < 0.05. Differences between slaughtering ages within the breed: C, D < 0.01; c, d: p < 0.05. L*, a* and b* are the symbols of the color indices, according the CIELab as explained in M&M.

2.5 Statistical analysis

Measured parameters were analyzed using a mixed model as follows:

$$y_{ijk} = \mu + B_i + SA_j + (BSA)_{ij} + F_k + \varepsilon_{ijk}$$

where μ is the overall mean, B represents the fixed effect of breed, SA the fixed effect of slaughter age, BSA their interaction, F the random effect of the farm and ε is the random error term. Within treatments, data were checked for outliers, which were not automatically rejected but only after checking plausibility. Body weight differences at the two slaughter ages have also been included in the analysis as a covariate. Pair wise comparisons were performed using Tukey's honest test at 0.05 significance level. The results are presented as least square means ± standard error of the means (pooled SEM). Data was analyzed using the STATGRAPHICS statistical software (2024) designed for Windows.

3 Results

3.1 Slaughtering and carcass traits of pigs

The live weights and dressing percentages of Apulo-Calabrese (AC) and Greek Pig (GP) slaughtered at 9 and 12 months of age are presented in Table 4. The live weight and the right-side carcass weight of the animals was significantly affected by the slaughter age ($p < 0.05$), as expected, but not by the breed. The hot dressing percentage was significantly greater in the Apulo-Calabrese pigs, regardless of the slaughtering age ($p < 0.01$), while the cold dressing percentage was affected neither by the slaughter age nor by the breed.

Table 5 presents the results of the dissection of the commercial meat cuts (shoulder, ham and loin) of the Apulo-Calabrese (AC) and Greek (GP) pigs. The breed had no significant effect on any of the meat cuts or their constituents (lean, fat, bone and rind). On the contrary, the slaughter age affected differently the proportion of the tissue components in the meat cuts examined. In the shoulder, a significantly lower amount of lean ($p < 0.01$) and fat ($p < 0.05$) was reported for pigs slaughtered at 12 months, in turn of a significantly higher incidence of the bone fraction ($p < 0.01$). Slaughtering at 12 months significantly lowered the percentage of lean ($p < 0.01$) while increasing the proportion of bone ($p < 0.01$) in the ham. The percentage of lean of the loin decreased ($p < 0.05$) with the delay of the slaughtering age only in the AC group. In both breeds, the percentage of fat markedly increased during growth ($p < 0.05$).

3.2 Physical properties and chemical composition of meat from the *Longissimus lumborum* muscle

In terms of meat quality, the breed did not affect any of the physical properties of the *Longissimus lumborum* muscle (Table 6). With regards to the slaughter age, when slaughtered at 12 months, meat showed significantly higher a* values ($p < 0.01$). All the chemical composition constituents were significantly affected by the genotype, meat from the AC breed showed markedly lower contents of moisture ($p < 0.05$) and fat ($p < 0.01$) as compared to GP, while significantly higher protein amount ($p < 0.01$). The ash content was markedly ($p < 0.05$) higher in the AC breed slaughtered

10.3389/fanim.2025.1656623

TABLE 7 Fatty acid profile of *Longissimus lumborum* muscle of Apulo-Calabrese (AC) and Greek (GP) autochthonous pig breeds slaughtered at 9 and 12 months of age.

Fatty Acids	AC		GP		SEM[1]	Effects[2]		
	9	12	9	12		B	SA	BxSA
C14:0	1.25^{C}	0.91^{D}	1.27	1.13	0.06	0.064	0.001	0.097
C15:0	0.042	0.040	0.051^{b}	0.064^{a}	0.04	0.031	0.155	0.056
C16:0	22.52^{b}	22.26	24.61^{a,c}	22.45^{d}	0.47	0.029	0.015	0.068
C17:0	0.07^{b}	0.05^{b}	0.35^{a}	0.37^{a}	0.03	0.001	0.944	0.576
C18:0	12.42^{C}	10.96^{D}	12.81^{C}	10.69^{D}	0.40	0.888	0.001	0.400
C20:0	0.08^{a}	0.09^{a}	0.05^{b}	0.06^{b}	0.01	0.027	0.543	0.899
C22:0	0.48	0.47	0.45	0.58	0.05	0.411	0.197	0.175
C14:1	0.04	0.02	0.04	0.01	0.02	0.899	0.269	0.981
C16:1	2.08^{D}	3.27^{C}	2.89^{D}	3.34^{C}	0.21	0.058	0.002	0.173
C17:1	0.21^{B}	0.15^{B}	0.31^{A}	0.34^{A}	0.02	0.001	0.489	0.055
C18:1n7	3.54^{D}	8.59^{A,C}	3.49	4.23^{B}	0.47	0.001	0.001	0.001
C18:1n9	40.44	38.26^{B}	41.88	42.73^{A}	0.63	0.001	0.345	0.030
C18:2n6t	0.13	0.05	0.08	0.13	0.01	0.166	0.179	0.001
C18:2n6c	11.99^{A}	10.31^{A}	7.27^{B}	8.44^{B}	0.91	0.002	0.086	0.189
C18:2cnjc	0.79	0.75	0.75	0.82	0.04	0.733	0.766	0.267
C18:2cnjt	0.03^{B}	0.07	0.10^{A}	0.07	0.01	0.003	0.894	0.002
C18:3n3	0.59^{B,C}	0.29^{B,D}	1.02^{A,C}	0.82^{A,D}	0.06	0.001	0.001	0.477
C18:3n6	0.03^{B}	0.07^{B}	0.24^{A}	0.31^{A}	0.03	0.001	0.061	0.589
C20:1n9	0.03^{B}	0.07^{B}	0.18^{A}	0.13^{A}	0.01	0.001	0.723	0.013
C20:2n6	0.52^{A}	0.32^{A}	0.05^{B}	0.05^{B}	0.05	0.001	0.069	0.066
C20:3n3	0.81^{b,D}	1.86^{a,C}	0.95^{a}	0.87^{b}	0.17	0.027	0.010	0.005
C20:3n6	0.14^{B}	0.21^{B}	0.53^{A,D}	1.26^{A,C}	0.10	0.001	0.001	0.005
C20:5n3	0.02^{B}	0.04^{B}	0.15^{A,D}	0.31^{A,C}	0.02	0.001	0.001	0.003
C22:5n3	0.15^{a}	0.20^{a}	0.08^{b}	0.13^{b}	0.03	0.020	0.068	0.955
C22:5n6	0.13	0.18	0.19	0.12	0.03	0.923	0.767	0.076
C22:6n3	0.07	0.08^{B}	0.08^{D}	0.13^{A,C}	0.01	0.002	0.001	0.058
Other Acids	1.41^{A,C}	0.45^{D}	0.16^{B}	0.43	0.02	0.002	0.001	0.051
SFA	36.91^{a,C}	34.77^{a,D}	39.63^{b,C}	35.36^{b,D}	0.68	0.029	0.001	0.137
MUFA	46.34^{D}	50.34^{C}	48.77^{D}	50.77^{C}	0.84	0.108	0.003	0.288
PUFA	15.34^{a}	14.44	11.44^{b}	13.44	1.09	0.041	0.645	0.197
UFA	61.68^{D}	64.78^{C}	60.21^{C}	64.21^{D}	0.60	0.116	0.001	0.453
n-6	13.74^{a}	11.96	9.17^{b}	11.19	0.96	0.013	0.926	0.065
n-3	1.63	2.47	2.28	2.28	0.21	0.367	0.068	0.067
n-6/n-3	8.48^{A,C}	5.26^{a,D}	4.07^{B}	4.93^{b}	0.55	0.001	0.048	0.002
SFA/PUFA	2.49^{b}	2.55	3.48^{a}	2.64	0.23	0.035	0.123	0.074
UFA/SFA	1.67^{d}	1.87^{c}	1.52^{d}	1.82^{c}	0.05	0.061	0.041	0.277

(Continued)

TABLE 7 Continued

Fatty Acids	AC		GP		SEM[1]	Effects[2]		
	9	12	9	12		B	SA	BxSA
AI	$0.45^{b,c}$	$0.40^{b,d}$	$0.49^{a,c}$	$0.42^{a,d}$	0.01	0.028	0.038	0.333
TI	$0.84^{B,c}$	$0.78^{B,d}$	$0.97^{A,c}$	$0.80^{A,d}$	0.03	0.009	0.044	0.051

[1]SEM, standard error of means. Differences between breed within each slaughtering age: A, B < 0.01; a, b, p < 0.05. Differences between slaughtering ages within the breed: C, D: < 0.01; c, d: p < 0.05.
SFA, Saturated fatty acids; MUFA, Mono-unsaturated fatty acids; PUFA, Poly-unsaturated fatty acids; UFA, unsaturated fatty acids.

at 9 months as compared to the GP groups, in turn of a lower N-free extract content ($p < 0.05$). The slaughter age affected a markedly greater moisture in both genotypes ($p < 0.05$) in turn of a lower fat content ($p < 0.05$). The N-free extract content was significantly greater in the AC pigs slaughtered at 12 months as compared to 9 ($p < 0.05$), while, adversely, this parameter decreased in GP slaughtered at 12 months ($p < 0.05$). A significant interaction between breed and slaughter age was recorded for the ash and the N-free extract content of the muscle.

3.3 Fatty acid profile of meat from the *Longissimus lumborum* muscle

Table 7 presents the fatty acid profile of the *Longissimus lumborum* muscle. In general, meat from the AC breed showed a lower content of total saturated fatty acids (SFA) at both slaughtering ages ($p < 0.05$) and a higher one of poly-unsaturated (PUFA) and of n-6 fatty acids ($p < 0.05$) when slaughtered at 9 months, while no differences were observed between breeds for the total n-3, monounsaturated (MUFA) and unsaturated (UFA) fatty acids. In both breeds, slaughtering at 12 months determined a decrease of the SFA content of the muscle while the MUFA and UFA concentrations were increased ($p < 0.01$). The food risk associated indices (AI and TI) were affected significantly both by the breed and the slaughter age: the AI and TI were lower in meat from the AC breed at both slaughtering ages ($p < 0.05$ and $p < 0.01$, respectively). In both breeds, the AI and TI indices significantly decreased by increasing the age at slaughter ($p < 0.05$).

3.4 Limitations to the study

This study compares carcass and meat quality parameters from two native black pig breeds, one Italian and one Greek, slaughtered at 9 and 12 months. Generally, comparing carcass and meat quality from different autochthonous genotypes is challenging due to the high variability between and within breeds (Pugliese and Sirtori, 2012; Sarmiento-García and Vieira-Aller, 2023), resulting from different management practices and environmental settings. Despite the great effort made to ensure similar rearing conditions in the two habitats, we are aware of the presence of some limitations.

In this preliminary study, we considered only one farm per country, recognizing the limited genetic variability of the animals and the lack of variability between farms. Despite extensive efforts to provide similar diets to level feeding differences, other confounding factors persist, including environmental differences (such as those concerning weather conditions and soil characteristics), although we chose the Italian and Greek farm in order to minimize these differences. As for animal management practices, that may have been affected by different interactions with livestock handlers, we had a day-by-day check of the farming conditions in the two farms in order to have a strict control of the factors we could intervene on. Furthermore, no observations on pig behavior were recorded during the trial, which could be useful for a more precise interpretation of the results regarding growth and slaughter performances.

It must be pointed out that there are several restrictions when working with autochthonous breeds, the most important being the distribution of small populations in many different herds. Based on the data available from the Domestic Animal Diversity Information System (DAD-IS) of the Food and Agriculture Organization of the United Nations (2014b), Greece has an average of 5000 autochthonous black pigs registered, reared in 56 herds, while in Italy there are about 5000 ApuloCalabrese pigs spread in 77 registered herds (ANAS, 2023). Native pig populations usually consist of a limited number of boars and sows with defined pedigree information, while phenotypic information is modest (Radović et al., 2017). The difficulty to ensure an adequate number of animals has also been reported in previous studies (Margeta et al., 2018), while other authors have investigated pig production from autochthonous breeds reared in intensive systems (Franci and Pugliese, 2007).

Despite the existing limitations described above, mainly the small number of animals and the lack of management homogeneity across holdings which may jeopardize the validity of the results, these challenges should not be a deterrent to conducting research on autochthonous breeds. Hence, although the statistics are challenging, this sort of research is required to generate knowledge on these less studied breeds. The preliminary results obtained in this study contribute to provide information on the meat quality of these two "neighboring" autochthonous breeds and could be used to design potential strategies for the enhancement of the yield and quality of their products.

4 Discussion

Autochthonous breeds are well adapted to the environmental conditions as a result of the evolutionary and selection processes, with higher resistance to disease and improved utilization of pasture than commercial hybrids (Sarmiento-García and and Vieira-Aller, 2023). The intake of small shrubs and other vegetative species carried out by indigenous grazing animals contributes to the prevention of fire (Szyndler-Nędza et al., 2021; Giannico et al., 2024). Rearing autochthonous breeds according to ecofriendly farming practices is perceived by consumers as being respectful for the animal welfare and the environment, thus improving a positive image of meat production and quality (García-Gudiño et al., 2021; Leite et al., 2022b).

Despite commercial hybrids demonstrate better productivity traits, their meat is usually characterized by poorer quality attributes (Sarmiento-García and Vieira-Aller, 2023), which include high drip loss, color loss, and lower intramuscular fat content (IMF), thus reducing the technological value of this meat for transformation into processed products (Leite et al., 2022a). One of the main differences between hybrids and autochthonous pigs regards the IMF and fatty acid profile of meat (Pugliese and Sirtori, 2012), which affect sensory attributes (such as juiciness or tenderness) and processing properties (Nevrkla et al., 2017). In the commercial swine industry, crossbreeding is common, using a limited number of breeds to produce F1 hybrids that take advantage of heterosis effects (Prasad and Laxmi, 2023). Autochthonous pig breeds are well-known for their rusticity, slow-growing, and they are usually slaughtered at an advanced age, providing meat with high nutritional properties (Bedia et al., 2012). Numerous studies have been carried out on several breeds in the Mediterranean basin, like the Iberian (Nieto et al., 2019; Tejeda et al., 2020), the Celta (Gómez and Lorenzo, 2013; Franco et al., 2014) in Spain, the Cinta Senese (Serra et al., 2014, 2018) and the Apulo-Calabrese (Aboagye et al., 2020; Scerra et al., 2024) in Italy and the Blanc de l'Ouest (Labroue et al., 2000; Renaudeau et al., 2005) in France.

The diet is considered one of the most crucial aspects which could modify the content and composition of fat (Benítez et al., 2016; Vieira et al., 2021) contributing to the production of healthier meats (Wood et al., 2004). Several studies have described how the lipid deposits of pigs are changed as a function of their nutrition (Poklukar et al., 2020; Tejeda et al., 2020; Scerra et al., 2024), even if genetics can play an important role in this (Franco et al., 2016). Therefore, these strategies would seem to be of more relevance in obtaining high-quality products derived from autochthonous breeds, such as those protected by brands, namely Protected Designation of Origin (PDO) or Protected Geographical Indication (PGI) (Kušec et al., 2022; Ferronato et al., 2023; Karolyi, 2024). These brands, as well as many regional or national ones (Kastelic and Čandek-Potokar, 2013; Cañás Bottos, 2020), perform an important role in marketing indigenous pork (Candek-Potokar et al., 2018), that can open up niche markets for this meat and raise awareness on their economic and social importance (Kasprzyk and Walenia, 2023).

As discussed by Jonsäll et al. (2001), the effects of the rearing system on the physical parameters of meat from "improved" pigs are contradictory. Even in studies on local breeds, the data reported are not always consistent. The higher value of meat shear force recorded in Cinta Senese pigs reared outdoors (Pugliese et al., 2005) was probably due to their older age at slaughter rather than to the rearing system; this hypothesis is confirmed by the fact that no differences in meat tenderness were found between Nero Siciliano pigs reared outdoors or indoors when slaughtered at the same age (Pugliese et al., 2004). The older age at slaughter of Cinta Senese pigs reared outdoors may also be the reason for their higher values of CIELab a* and, consequently, of chroma, with respect to pigs reared indoors. In fact, as reported by Mayoral et al. (1999), myoglobin concentration in pig muscle increases with age. Very few differences were found by Lopez-Bote et al. (2008) in drip loss, heme pigment concentration, CIELab colour or rheological properties in *Psoas major* muscle between sedentary and free-range Iberian pigs, thus suggesting that the intensity of the exercise is not high enough to affect fresh meat quality characteristics. The lipid composition of pork includes 568 different lipid species with 139 triglycerides (TAG). There are three types of fatty acids in TAG, including saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA) (Yi et al., 2023). According to the current health recommendations proposed by the European Food Safety Authority (EFSA, 2010), the diet should be rich in PUFA and MUFA and low in SFA due to the apparent relationship between plasma cholesterol and cardiovascular disease (Dugan et al., 2015). In pork, IMF ranged between 2% to 15%, which constitutes about 35–40% of SFA, being C14:0 the major fatty acid. Based on the above information, many recommendations have been proposed to reduce the intake of red meat, such as pork. In response, several studies have focused their efforts on examining the content and composition of pork fat, and different strategies to modify it. These findings have shown that composition and the deposition of fat in pork could vary with genetics, with important differences between commercial and indigenous pigs. For example, the experiment carried out by Nevrkla et al. (2017) with Prestice Black-Pied (an indigenous Czech breed) showed a decrease in SFA (C8:0, C10:0, C15:0, C22:0) and an increase in MUFA (mainly in C18:1 n-9) content, which is consistent with the findings of Tomović et al. (2016) for white Mangalica pigs (an indigenous Hungarian pig). In the same line, Kušec et al. (2022) compared Black Slavonian barrows with commercial hybrids, and they observed a decrease in palmitic acid (C16:0) and an increase in beneficial unsaturated fatty acids, such as palmitoleic acid (C16:1 n-7), oleic acid (C18:1 n-9), gamma-linoleic acid (C18:3 n6), and nervonic acid (24:1 n-9), which increase MUFA and PUFA n-3 content. Similar trends have been reported by Serra et al. (2014), who reported higher MUFA content in the Cinta Senese Italian breed than in industrial pigs (Large White). Teixeira and Rodrigues (2021) described higher contents of MUFA (C18:1 n-9, C16:0, and C11:1 n-7) in the Preto Alentejano breed (a South-Portuguese pig) than in commercial hybrid while inconclusive differences were found in PUFA. Related tendencies have been described by Lebret et al. (2014), who showed a decrease in SFA for Basque Pork (non-selected, local French pig breed) compared to Large White (hybrid pig) which coincides with those described for Iberian pork (Robina et al., 2013).

Noticeable differences in the concentration of individual fatty acids may be observed across breeds due to differentially expressed genes and polymorphisms which can contribute to meat overall quality (Valdés-Hernández et al., 2025). For example, the oleic acid content has been positively correlated with pork meat flavor, while the percentage of stearic acid has been associated with fat firmness. A high IMF and oleic acid content has been reported in both raw meat and dry-cured products of Iberian pigs feed by grass and acorns during the fattening period, being an indicator of its quality (Ruiz-Carrascal et al., 2000). In this study, meat from Greek pigs slaughtered at 12 months showed an increased oleic acid content as compared to the Apulo-Calabrese breed. Furthermore, it has been reported that the intramuscular oleic-to-stearic fatty acid ratio (C18:1n-9/C18:0) is an important indicator of the biosynthesis and desaturation of fatty acids in muscle. In this study, though the concentration of stearic acid was unaffected by the genotype, in both breeds it significantly decreased as the slaughter age increased, with benefits for meat healthiness, since the concentration of stearic acid affects the index of thrombogenicity. As experienced on Chinese local breeds (Xu et al., 2025), the application of lipidomics and volatilomics analysis may help to provide information on genetic differences in terms of cellular lipids and volatile compounds content and their relationship to meat flavor.

In addition to the influence of the proportion of PUFA, MUFA and SFA to obtain a healthy product, the ratio of n-6/n-3 has a great nutritional significance (Turner et al., 2014; Dugan et al., 2015), especially with regards to the content of eicosapentaenoic acid (EPA), docosapentaenoic acid (DPA), and docosahexaenoic acid (DHA) (Jaturasitha et al., 2016), being necessary for the equilibrated biosynthesis of eicosanoids in the organism. Unbalanced n-6/n-3 ratios, which should be less than either 4:1 or 5:1 (Jaturasitha et al., 2016), have been linked to many disorders, including cardio-vascular and inflammatory diseases or diabetes (Wood et al., 2004). Furman et al. (2010) showed a better n-6/n-3 ratio for Krškopolje (a Slovenian indigenous pig breed) than in hybrid pork, which is consistent with the findings observed by Nevrkla et al. (2017) and Kušec et al. (2022) for Prestice Black-Pied pork and Black Slavonian, respectively.

Atherogenic (AI) and thrombogenic (TI) indices have been described as important markers in identifying healthy products, since lower values demonstrate a decrease in SFA to unsaturated acids (Cebulska et al., 2018; Leite et al., 2022a). AI and TI values less than 0.5 and 1.2, respectively, have been documented in indigenous breeds than in commercial hybrids (Cebulska et al., 2018). In this study, both breeds provided satisfactory values of these indices, especially when pigs were slaughtered at 12 rather than 9 months.

5 Conclusions

Autochthonous pigs are a valuable genetic reserve that can be used to recover the organoleptic properties of pig meat, properties that are lost because of severe selective programs undertaken to improve pig production. Our results highlight that better live weights and slaughtering yields, improved carcass conformation, lower refrigeration losses, greater decrease of pH and a greater incidence of the loin and shoulder, were obtained when slaughtering is performed at 12 months of age. Moreover, at this age, a superior lean content of these two meat cuts, along with better tenderness and a favorable chemical and fatty acid composition were also recorded. Even though the Greek pig is one of the oldest breeds found in Greece, there is lack of information about its phenotypic and production characterization. Future studies of this breed may facilitate the development and rational control of breeding programs and provide knowledge of the historical basis which gives foundation to the origin and evolution of breeds. Greece has committed to international treaties to create the necessary infrastructure and to prepare the necessary national strategy for the development of actions to protect, preserve and utilize genetic resources and agricultural biodiversity and to participate in cooperation networks at national, regional and global level. These studies will make a decisive contribution to the rescue of the autochthonous breed of the black pig, which is valuable for Mediterranean countries, to the protection and preservation of biodiversity as well as to the increase of the productivity of the farmed animals of this breed.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Ethics Committee of the Hellenic Agricultural Organization (ELGO-DIMITRA) (445/14-6-2022). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

DK: Conceptualization, Investigation, Resources, Project administration, Writing – original draft, Methodology, Writing – review & editing. GS: Software, Writing – original draft, Data curation. GM: Supervision, Writing – original draft. EA: Formal Analysis, Writing – original draft, Investigation. ST: Investigation, Writing – original draft, Conceptualization, Data curation, Formal Analysis, Methodology, Writing – review & editing. FG: Investigation, Resources, Funding acquisition, Writing – original draft. MC: Visualization, Validation, Writing – original draft, Supervision, Investigation, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research and/or publication of this article. Part of this research was funded by the GREEN FUND GREECE, grant number 003141, and the other was carried out within the Agritech National Research Center and received funding from the European Union Next-Generation EU (PIANO NAZIONALE DI RIPRESA E RESILIENZA (PNRR) – MISSIONE 4 COMPONENTE 2, INVESTIMENTO 1.4 – D.D. 1032 17/06/2022, CN00000022; Agritech Unique Project Code (CUP):

H93C22000440007). This manuscript reflects only the authors' views and opinions, neither the European Union nor the European Commission can be considered responsible for them.

Acknowledgments

The authors express their gratitude to the farmers who collaborated in this project in Greece (Dimitris Dimos and Douma farm), to Dr. Francesco Carriero of "Salumi Martina Franca" and Dr. Canio Abbate of the "Pian del Camino" farms in Italy. The authors also thank the technicians from the Department of Soil, Plant and Food Sciences Massimo Lacitignola, Nicolò De Vito and Domenico Gerardi for their laboratory assistance.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

References

Aboagye, G., Zappaterra, M., Pasini, F., Dall'Olio, S., Davoli, R., and Costa, L. N. (2020). Fatty acid composition of the intramuscular fat in the *Longissimus thoracis* muscle of Apulo-Calabrese and crossbreed pigs. *Livestock Sci* 232, 103878. doi: 10.1016/j.livsci.2019.103878

ANAS. (2023). ANAS Libro Genealogico Suini. Available online at: https://www.anas.it/html/lg_v2_01.htm (Accessed February 21, 2025).

ANAS. (2025). Libro Genealogico Suini. Available online at: https://www.anas.it/cgi-bin/exe/allevisc.exe?trans=A0&Tipo=BE (Accessed August 08, 2025).

Antikas, T. (2003). "Pigs in Greece: From Boar (ing) Myths to Pig Epitaphs" in *Proceedings of the International Conference—Pigs and Humans, Durham, UK*. pp. 26–29.

Apulian Region (2007). Linee guida applicative in materia di promozione e riconoscimento dei distretti produttivi. Available online at: https://portale2015.consiglio.puglia.it/documentazione/leges/modulo.aspx?id=11746 (Accessed June 5, 2025).

Apulian Region (2017). Disciplina dell'attività di lobbying presso i decisori pubblici. Available online at: https://welforum.it/wp-content/uploads/2017/11/Puglia_LR_30_2017.pdf (Accessed June 5, 2025).

Apulian Region (2024). Disposizioni per la formazione del bilancio di previsione 2025 e bilancio pluriennale 2025–2027 della Regione Puglia (legge di stabilità regionale 2025). Available online at: https://burp.regione.puglia.it/documents/20135/2427292/LR_42_2024.pdf/9b60b5ce-a37e-80b7-93f1cf6ac6ab0ec4?version=1.0&t=1735673810402 (Accessed June 5, 2025).

AOAC (2023). Official Methods of Analysis. Available online at: https://www.aoac.org/officialmethods-of-analysis/ (Accessed October 28, 2024).

Bedia, M., Serrano, R., and Bañón, S. (2012). Use of rustic pigs to manufacture pork salami free of colour and taste enhancers. *Ital. J. Food Sci.* 24, 24–2012.

Benítez, R., Núñez, Y., Fernández, A., Isabel, B., Rodríguez, C., Daza, A., et al. (2016). Adipose tissue transcriptional response of lipid metabolism genes in growing iberian pigs fed oleic acid v. *Carbohydr. Enriched Diets. Anim.* 10, 939–946. doi: 10.1017/S1751731115003055

Bittante, G. (2011). Italian animal genetic resources in the Domestic Animal Diversity Information System of FAO. *Ital. J. Anim. Sci* 10, 151–158. doi: 10.4081/ijas.2011.e29

Bondoc, O. L. (2015). "Organic livestock farming and breeding toward food security of smallholder farmers in the tropics," in *Discussion Paper Series - Southeast Asian Regional Center for Graduate Study and Research in Agriculture (SEARCA), No.2015* (Los Baños: English Bulletin, Philippines). doi: 10.5555/20163061433

Bozzi, R., Gallo, M., Geraci, C., Fontanesi, L., and Batorek-Lukač, N. (2019). "Apulo-Calabrese Pig," in *European Local Pig Breeds-Diversity and Performance. A study of project TREASURE*. eds. M. Candek-Potokar and R. M Nieto Linan. (London, UK: IntechOpen), 65–72.

Cañás Bottos, L. (2020). Race and Process: certifying iberian pigs and invisibilising humans. *Norsk antropologisk tidsskrift* 30, 258–273. doi: 10.18261/issn.1504-2898-2019-03-04-06

Candek-Potokar, M., Giusto, A., Conti, C., Cosola, C., and Fontanesi, L. (2018). Improving sustainability of local pig breeds using quality labels–case review and trademark development in project TREASURE. *Archivos zootecnia* 1), 235–238.

Cebulska, A., Václavková, E., Bocian, M., Dybała, J., Wiśniewska, J., and Kapelański, W. (2018). Quality and dietary value of pork meat of the puławska and złotnicka spotted breeds, and commercial fattening pigs. *Ann. Anim. Sci.* 18, 281–291. doi: 10.1515/aoas-2017-0033

Christie, W. W. (1982). *Lipid Analysis-Isolation, Separation, Identification and Structural Analysis of Lipids* (Oxford, UK: Pergamon), 270.

Colonna, M. A., Tarricone, S., Giannico, F., Selvaggi, M., Carriero, F., Crupi, P., et al. (2021). Dietary effects of extra virgin olive oil extracted by ultrasound technology or refined olive oil on the quality traits of pork and "Capocollo di martina franca" Dry-Cured Meat. *Animals* 11, 954. doi: 10.3390/ani11040954

Dugan, M. E. R., Vahmani, P., Turner, T. D., Mapiye, C., Juárez, M., Prieto, N., et al. (2015). Pork as a source of omega-3 (n-3) fatty acids. *J. Clin. Med.* 4, 1999–2011. doi: 10.3390/jcm4121956

EFSA (2010). *Panel on Dietetic Products Nutrition and Allergies. Scientific Opinion on Dietary Reference Values for Fats, Including Saturated Fatty Acids, Polyunsaturated Fatty Acids, Monounsaturated Fatty Acids, Trans Fatty Acids, and Cholesterol* Vol. 8 (John Wiley & Sons (Wiley) in Hoboken, New Jersey, USA: EFSA), 107.

European Parliament (2009). Regulation (EC) No 1099/2009 on the protection of animals at the time of killing. Available online at: https://eur-lex.europa.eu/EN/legalcontent/summary/protection-of-animals-at-the-time-of-killing.html (Accessed October 28, 2024).

European Parliament (2010). Directive - 2010/63 - EN - EUR-Lex. Available online at: https://eur-lex.europa.eu/eli/dir/2010/63/oj (Accessed October 27, 2024).

European Parliament (2018). Regulation (EU) 2018/848 of the European Parliament and of the Council of 30 May 2018 on organic production and labelling of organic products and repealing Council Regulation (EC) No 834/2007. Available online at: https://eur-lex.europa.eu/eli/reg/2018/848/oj/eng (Accessed October 12, 2024).

Ferronato, G., Froldi, F., and Prandini, A. (2023). "The Quality of Heavy Pork Meat: The Role of PDO Production Specifications," in *Sustainable Transition of Meat and Cured Meat Supply Chain: A Transdisciplinary Approach* (Springer Nature Switzerland, Cham), 73–83.

Folch, J., Lees, M., and Sloane Stanley, G. H. (1957). A simple method for the isolation and purification of total lipides from animal tissues. *J. Biol. Chem.* 226, 497–509. doi: 10.1016/S0021-9258(18)64849-5

Food and Agriculture Organization of the United Nations. (2014a). Forage Resources and Ecosystem Services Provided by Mountain and Mediterranean Grasslands and Rangelands. FAO Available online at: https://www.fao.org/family-farming/detail/en/c/326869/2014 (Accessed October 27, 2024).

Food and Agriculture Organization of the United Nations. (2014b). Domestic Animal Diversity Information System (DAD-IS). Available online at: https://www.fao.org/dad-is/en/ (Accessed October 27, 2024).

Franci, O., and Pugliese, C. (2007). Italian autochthonous pigs: progress report and research perspectives. *Ital. J. Anim. Sci* 6, 663–671. doi: 10.4081/ijas.2007.1s.663

Franco, D., Carballo, J., Bermñudez, R., and Lorenzo, J. M. (2016). Effect of genotype and slaughter age on carcass traits and meat quality of the Celta pig breed in extensive system. *Ann. Anim. Sci* 16, 259. doi: 10.1016/j.meatsci.2013.06.024

Franco, D., Vazquez, J. A., and Lorenzo, J. M. (2014). Growth performance, carcass and meat quality of the celta pig crossbred with duroc and landrance genotypes. *Meat Sci.* 96, 195–202. doi: 10.1016/j.meatsci.2013.06.024

Furman, M., Malovrh, S., Levart, A., and Kovač, M. (2010). Fatty acid composition of meat and adipose tissue from krškopolje pigs and commercial fatteners in Slovenia. *Arch. Anim. Breed.* 53, 73–84. doi: 10.5194/aab-53-73-2010

García-Gudiño, J., Blanco-Penedo, I., Gispert, M., Brun, A., Perea, J., and Font-i-Furnols, M. (2021). Understanding consumers' Perceptions towards iberian pig production and animal welfare. *Meat Sci.* 172, 108317. doi: 10.1016/j.meatsci.2020.108317

Giannico, F., Karatosidi, D., Carbonara, C., Ragni, M., Tarricone, S., Caputi Jambrenghi, A., et al. (2024). Effects of grazing on grassland or wood-pasture, slaughtering age and ageing time on meat production and quality in Podolian young bulls. *Veterinary Q.* 44, 1–12. doi: 10.1080/01652176.2021.2381544

Golovina, S., Kuznetsova, A., Akhmetiyanova, A., Kuznetsov, A., and Zholdoyakova, G. (2025). "Prospects for organic agriculture development in the context of modern challenges and opportunities," in *BIO Web of Conferences*, vol. 179. (Les Ulis, France: EDP Sciences), 07001. doi: 10.1051/bioconf/202517907001

Gómez, M., and Lorenzo, J. M. (2013). Effect of fat level on physicochemical, volatile compounds and sensory characteristics of dry-ripened "Chorizo" Celta Pig Breed. *Meat Sci.* 95, 658–666. doi: 10.1016/j.meatsci.2013.06.005

Goracci, J., and Camilli, F. (2025). Agroforestry and animal husbandry. *Anim. Husbandry-Beliefs Facts Reality: Beliefs Facts Reality* 201, 201-218. doi: 10.5772/intechopen.1006711

Jaturasitha, S., Chaiwang, N., Kayan, A., and Kreuzer, M. (2016). Nutritional strategies to improve the lipid composition of meat, with emphasis on Thailand and asia. *Meat Sci.* 120, 157–166. doi: 10.1016/j.meatsci.2016.04.014

Jonsäll, A., Joansson, L., and Ludström, K. (2001). Sensory quality and cooking loss of ham muscle (M. *Biceps femoris*) from pigs reared indoors and outdoors. *Meat Sci* 57, 245–250. doi: 10.1016/S0309-1740(00)00097-8

Karolyi, D. (2024). "Supporting the preservation of local pig breeds through EU quality schemes–an overview of geographical indications for fresh and processed pork," in *7th Fatty Pig & 12th Mediterranean Pig Meeting* (Budapest, Hungary: University of Veterinary Medicine).

Kasprzyk, A., and Walenia, A. (2023). Native pig breeds as a source of biodiversity—breeding and economic aspects. *Agriculture* 13, 1528. doi: 10.3390/agriculture13081528

Kastelic, A., and Čandek-Potokar, M. (2013). Application of quality labels in support of conservation of local breeds—A challenge for Slovenian Krškopolje pig. *Acta Agric. Slov* 4, 205–209. doi: 10.14720/aas-s.2013.4.19055

Kušec, G., Komlenić, M., Gvozdanović, K., Sili, V., Krvavica, M., Radišić, Ž., et al. (2022). Carcass composition and physicochemical characteristics of meat from pork chains based on native and hybrid pigs. *Processes* 10, 370. doi: 10.3390/pr10020370

Labroue, F., Goumy, S., Gruand, J., Mourot, J., Neelz, V., and Legault, C. (2000). Comparaison au Large White de quatre races locales porcines françaises pour les performances de croissance, de carcasse et de qualité de la viande. *Journées Recherche Porcine en France* 32, 403–411.

Labroue, F., Marsac, H., Luquet, M., Gruand, J., Mourot, J., Neelz, V., et al. (2001). "Performances of French Local Breeds", in *Pig genetic resources in Europe: characterisation and conservation*, eds. L. Ollivier, F. Labroue, G. Gandini and J. V. Delgrado (Wageningen, Netherlands: Wageningen Pers), 51–57.

Lebret, B., Dourmad, J. Y., Mourot, J., Pollet, P. Y., and Gondret, F. (2014). Production performance, carcass composition, and adipose tissue traits of heavy pigs: influence of breed and production system. *J. Anim. Sci.* 92, 3543–3556. doi: 10.2527/jas.2013-7398

Leite, A., Domínguez, R., Vasconcelos, L., Ferreira, I., Pereira, E., Pinheiro, V., et al. (2022a). Can the introduction of different olive cakes affect the carcass, meat and fat quality of bisaro pork? *Foods* 11, 1650. doi: 10.3390/foods11111650

Leite, A., Vasconcelos, L., Ferreira, I., Sarmiento-García, A., Domínguez, R., Santos, E. M., et al. (2022b). Chemical, physicochemical and sensorial characterization of nitrite-free dry-cured bísaro shoulders. *Foods* 11, 3079. doi: 10.3390/foods11193079

Lopez-Bote, C. J., Toldrà, F., Daza, A., Ferrer, J. M., Menoyo, D., Siliò, L., et al. (2008). Effect of exercise on skeletal muscle proteolytic enzyme activity and meat quality characteristics in Iberian pigs. *Meat Sci* 79, 71–76. doi: 10.1016/j.meatsci.2007.08.002

Margeta, P., Gvozdanovic, K., Kušec, I. D., Radišić, Ž., Kusek, G., and Margeta, V. (2018). Genetic analysis of Croatian autochthonous pig breeds based on microsatellite markers. *Archivos Zootecnia* 1), 13–16. doi: 10.21071/az.v67iSupplement.3563

Mayoral, A. I., Dorado, M., Guillén, M. T., Robina, A., Vivo, J. M., Vazquez, C., et al. (1999). Development of meat and carcass quality characteristics in Iberian pigs reared outdoors. *Meat Sci* 52, 315–324. doi: 10.1016/S0309-1740(99)00008-X

Michailidou, S., Kalivas, A., Ganopoulos, I., Stea, E., Michailidis, G., Tsaftaris, A., et al. (2014). A multi-farm assessment of greek black pig genetic diversity using microsatellite molecular markers. *Genet. Mol. Res.* 13, 2752–2765. doi: 10.4238/2014.April.14.4

Nevrkla, P., Kapelański, W., Václavková, E., Hadaš, Z., Cebulska, A., and Horký, P. (2017). Meat quality and fatty acid profile of pork and backfat from an indigenous breed and a commercial hybrid of pigs. *Ann. Anim. Sci.* 17, 1215–1227. doi: 10.1515/aoas-2017-0014

Nieto, R., García-Casco, J., Lara, L., Palma-Granados, P., Izquierdo, M., Hernandez, F., et al. (2019). "Ibérico (Iberian) Pig," in *European Local Pig Breeds—Diversity and Performance. A Study of Project TREASURE* (IntechOpen, London, UK).

Ortiz, A., González, E., García-Torres, S., Gaspar, P., and Tejerina, D. (2021). Do animal slaughter age and pre-cure freezing have a significant impact on the quality of iberian dry-cured pork loin? *Meat Sci* 179, 108531. doi: 10.1016/j.meatsci.2021.108531

Papatsiros, V. G., Tassis, P. D., Christodoulopoulos, G., Boutsini, S., Tsirigotakis, G., and Tzika, E. D. (2012). Health and production of Greek organic pig farming: Current situation and perspectives. *J. Hellenic Veterinary Med. Soc.* 63, 37–44. doi: 10.12681/jhvms.15396

Poklukar, K., Čandek-Potokar, M., Batorek Lukač, N., and Škrlep, M. (2020). Lipid deposition and metabolism in local and modern pig breeds: A review. *Animals* 10, 424. doi: 10.3390/ani10030424

Prasad, R. M. V., and Laxmi, P. J. (2023). "Concept of modern animal Management-Farm Animal Welfare," in *Recent Advances in Agricultural Sciences and Technology* (Ariana Publishers & Distributors, New Delhi (India).

Pugliese, C., Bozzi, R., Campodoni, G., Acciaioli, A., Franci, O., and Gandini, G. (2005). Performance of Cinta Senese pigs reared outdoors and indoors. 1. Meat and subcutaneous fat characteristics. *Meat Sci* 69, 459–464. doi: 10.1016/j.meatsci.2004.09.001

Pugliese, C., Calagna, G., Chiofalo, V., Moretti, V., Margiotta, S., Franci, O., et al. (2004). Comparison of the performances of Nero Siciliano pigs reared indoors and outdoors. 2. Joints composition, meat and fat traits. *Meat Sci* 68, 523–528. doi: 10.1016/j.meatsci.2004.02.020

Pugliese, C., and Sirtori, F. (2012). Quality of meat and meat products produced from southern european pig breeds. *Meat Sci.* 90, 511–518. doi: 10.1016/j.meatsci.2011.09.019

Radović, Č., Petrović, M., Katanić, N., Radojković, D. D., Savić, R., Gogić, M., et al. (2017). Fertility traits of autochthonous breeds of Mangalitsa, Moravka and Resavka. *Biotechnol. Anim. Husbandry* 33, 389–396. doi: 10.2298/BAH1704389R

Razmaitė, V., Šveistienė, R., Jatkauskienė, V., and Šiukščius, A. (2022). Pork consumption frequencies, attitudes and sensory acceptance of traditional products in Lithuania. *Foods* 11, 3292. doi: 10.3390/foods11203292

Renaudeau, D., Hilaire, M., and Mourot, J. (2005). A comparison of carcass and meat quality characteristics of Creole and Large White pigs slaughtered at 150 days of age. *Anim. Res.* 54, 43–54. doi: 10.1051/animres:2004042

Ribani, A., Taurisano, V., Karatosidi, D., Schiavo, G., Bovo, S., Bertolini, F., et al. (2023). Signatures of admixture and genetic uniqueness in the autochthonous greek black pig breed deduced from gene polymorphisms affecting domestication-derived traits. *Animals* 13, 1763. doi: 10.3390/ani13111763

Robina, A., Viguera, J., Perez-Palacios, T., Mayoral, A. I., Vivo, J. M., Guillen, M. T., et al. (2013). Carcass and meat quality traits of iberian pigs as affected by sex and crossbreeding with different duroc genetic lines. *Span. J. Agric. Res.* 11, 1057–1067. doi: 10.5424/sjar/2013114-4637

Ruiz-Carrascal, J., Ventanas, J., Cava, R., Andrés, A. I., and García, C. (2000). Texture and appearance of dry cured ham as affected by fat content and fatty acid composition. *Food Res. Int.* 33 (2), 91–95. doi: 10.1016/S0963-9969(99)00153-2

Sarmiento-García, A., and Vieira-Aller, C. (2023). Improving fatty acid profile in native breed pigs using dietary strategies: A review. *Animals* 13, 1696. doi: 10.3390/ani13101696

Scerra, M., Foti, F., Caparra, P., Cilione, C., Bognanno, M., Paolo, F., et al. (2024). Effects of feeding bergamot pulp and olive leaves on performance and meat quality in Apulo-Calabrese pigs. *Veterinary Anim. Sci* 23, 100336. doi: 10.1016/j.vas.2024.100336

Serra, A., Buccioni, A., Rodriguez-Estrada, M. T., Conte, G., Cappucci, A., and Mele, M. (2014). Fatty acid composition, oxidation status and volatile organic compounds in "Colonnata" Lard from large white or cinta senese pigs as affected by curing time. *Meat Sci.* 97, 504–512. doi: 10.1016/j.meatsci.2014.03.002

StatGraphics (2024). Inc, S.T Centurion product details: powerful statistical software package. Available online at: https://www.statgraphics.com/centurion-overview (Accessed October 28, 2024).

Serra, A., Conte, G., Giovannetti, M., Casarosa, L., Agnolucci, M., Ciucci, F., et al. (2018). Olive pomace in diet limits lipid peroxidation of sausages from cinta senese swine. *Eur. J. Lipid Sci. Technol.* 120, 1700236. doi: 10.1002/ejlt.201700236

Szyndler-Nędza, M., Światkiewicz, M., Migdał, Ł., and Migdał, W. (2021). The quality and healthPromoting value of meat from pigs of the native breed as the effect of extensive feeding with acorns. *Animals* 11, 789. doi: 10.3390/ani11030789

Tarricone, S., Colonna, M. A., Giannico, F., Ragni, M., Lestingi, A., and Facciolongo, A. M. (2019). Effect of an extruded linseed diet on meat quality traits in Nero Lucano pigs. *South Afr. J. Anim. Sci* 49, 1093–1103. doi: 10.4314/sajas.v49i6.13

Teixeira, A., and Rodrigues, S. (2021). Consumer perceptions towards healthier meat products. *Curr. Opin. Food Sci.* 38, 147–154. doi: 10.1016/j.cofs.2020.12.004

Tejeda, J. F., Hernández-Matamoros, A., Paniagua, M., and González, E. (2020). Effect of free-range and low-protein concentrated diets on growth performance, carcass traits, and meat composition of iberian pig. *Animals* 10, 273. doi: 10.3390/ani10020273

Tomović, V. M., Šević, R., Jokanović, M., Šojić, B., Škaljac, S., Tasić, T., et al. (2016). Quality Traits of Longissimus lumborum Muscle from White Mangalica, Duroc × White Mangalica and Large White Pigs Reared under Intensive Conditions and Slaughtered at 150 kg Live Weight: A Comparative Study. *Arch. Anim. Breed.* 59, 401–415. doi: 10.5194/aab-59-401-2016

Turner, T. D., Mapiye, C., Aalhus, J. L., Beaulieu, A. D., Patience, J. F., Zijlstra, R. T., et al. (2014). Flaxseed fed pork: N-3 fatty acid enrichment and contribution to dietary recommendations. *Meat Sci.* 96, 541–547. doi: 10.1016/j.meatsci.2013.08.021

Ulbricht, T. L. V., and Southgate, D. A. T. (1991). Coronary heart disease: seven dietary factors. *Lancet* 338, 985–992. doi: 10.1016/0140-6736(91)91846-M

Valdés-Hernández, J., Ramayo-Caldas, Y., Passols, M., Criado-Mesas, L., Castelló, A., Sánchez, A., et al. (2025). Identification of differentially expressed genes and polymorphisms related to intramuscular oleic-to-stearic fatty acid ratio in pigs. *Anim. Genet.* 56, e13491. doi: 10.1111/age.13491

Vieira, C., Sarmiento-García, A., García, J., Rubio, B., and Mart, B. (2021). Quality and shelf life of fresh meat from iberian pigs as affected by a new form of presentation of oleic acid and an organic-acid mix in the diet. *Foods* 10, 985. doi: 10.3390/foods10050985

Wood, J. D., Richardson, R. I., Nute, G. R., Fisher, A. V., Campo, M. M., Kasapidou, E., et al. (2004). Effects of fatty acids on meat quality: A review. *Meat Sci.* 66, 21–32. doi: 10.1016/S03091740(03)00022-6

Xu, S., Zheng, W., Zeng, Y., Tian, X., and Xu, X. (2025). Analysis of volatile flavor and lipids in different breeds of pork using electronic noses, GC–MS and UPLC-MS/MS. *J. Chromatogr. A* 1746, 465783. doi: 10.1016/j.chroma.2025.465783

Yi, W., Huang, Q., Wang, Y., and Shan, T. (2023). Lipo-nutritional quality of pork: the lipid composition, regulation, and molecular mechanisms of fatty acid deposition. *Anim. Nutr.* 13, 373–385. doi: 10.1016/j.aninu.2023.03.001