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ABSTRACT

A recent long-term system-level experiment, using grassland-based organic systems established as separate farmlets, showed that combining sheep and beef cattle within a mixed (**MIX**) system promoted self-sufficient production of grass-fed meat and improved economic and environmental performance in the sheep enterprise compared to a sheep-only (**SH**) system. In the present study, we used all male lambs produced over the first year in this experiment to evaluate the effect of this farming practice on some lamb carcass and meat sensory quality traits. Lambing took place at the end of February and lambs were pasture-fed from 1 month of age on average until slaughter, unless they were not ready for slaughter at 3–4 weeks before the start of the mating period in October, in which case they were finished indoors on a concentrate-based diet. All MIX lambs (n = 33) were finished at pasture. One SH lamb (out of a total of 85) had to be finished indoors with a concentrate-based diet. MIX lambs had a higher growth rate than SH lambs ($P < 0.001$), resulting in a lower lamb age at slaughter in MIX than in SH (150 vs 173 days, $P < 0.001$). Carcass weight and degree of fatness, kidney fat weight and dorsal fat thickness did not differ between systems. Kidney fat skatole concentration was higher in MIX than in SH (median value reaching 0.15 µg/g liquid fat and 0.11 µg/g liquid fat in MIX and SH, respectively, $P < 0.05$). This was most likely due to MIX lambs being slaughtered at a younger age and therefore eating younger grass. There were minor differences between MIX and SH lambs in dorsal fat firmness and in colour coordinates of *longissimus thoracis et lumborum* muscle. We conclude that while combining sheep and beef cattle within a mixed system offers advantages in terms of self-sufficient production of grass-fed meat and system economic and environmental performance, it could come at a cost to lamb flavour.

Implications

Even though combining sheep and beef cattle within a mixed pasture-based system favours the production of grass-fed lamb meat and has advantages for system self-sufficiency, economic and environmental performance and feed-food competition, it can also come at a cost to certain lamb meat sensory quality attributes, particularly flavour. Indeed, lambs from the mixed system combining sheep and beef cattle showed an increase in fat concentrations of skatole, a faecal-smelling compound, which in turn increases the risk of excessive flavour in lamb and could turn away consumers.

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Introduction

A recent long-term system-level experiment showed that combining sheep and beef cattle in a grassland-based mixed organic system promoted self-sufficient production of grass-fed lamb meat (Prache et al., 2023) and improved economic and environmental performance and feed-food competition in the sheep enterprise (Benoit et al., 2023). This was due to better animal performance and reduced use of inputs (Prache et al., 2023; Benoit et al., 2023). However, a fully comprehensive evaluation of this farming practice requires further consideration of the quality of the meat produced.

Using a subset of young cattle produced in this long-term experiment (all the animals produced over one year), Liu et al. (2022 and 2023) showed that there were no differences in beef quality between the mixed vs the beef cattle-only system.

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However, the scientific literature converges on the fact that combining sheep with beef cattle has no effect on calf growth performance but leads to faster lamb growth rate (d'Alexis et al., 2014; Jerrentrup et al., 2020; Barn et al., 2022; Prache et al., 2023), thereby reducing both the age of lambs at slaughter and the proportion of lambs finished indoors (Prache et al., 2023), which may have an impact on lamb meat quality (Prache et al., 2022). The improvement in lamb performance has been attributed to both a dilution of parasite burden, which young lambs are particularly sensitive to (Prache and Thériez, 1988), and a better nutritive value of the sward, especially its CP content and organic matter digestibility (Martin et al., 2020). Outcomes from recent studies show that the dilution of parasite burden is probably the most impactful factor (Joly et al., 2022; Prache et al., 2023). However, to the authors' knowledge, no studies have yet been published on the effects of combining sheep and beef cattle in a mixed pasture-based system on lamb carcass and meat quality.

Speeding up the growth rate of pasture-fed lambs by offering them a high (vs low) availability of good-quality pasture herbage has been shown to reinforce the beneficial impact of pasture-feeding on the nutritional value of meat fatty acids (**FAs**), by significantly increasing n-3 poly-unsaturated FA (**PUFA**) (+15%), n-6 PUFA (+16%) and conjugated linoleic acid (+20%) content and decreasing saturated FA (−3%) content (thus leading to a higher value of the PUFA/saturated FA ratio (+17%)), without changing *trans*-mono-unsaturated FA content in *Longissimus thoracis et lumborum* (**LTL**) muscle (Bauchart et al., 2012). From a human health standpoint, some saturated FAs and *trans*-mono-unsaturated FAs have been found to be associated with increased risks for cardiovascular disease (Chikwanha et al., 2018). On the other hand, n-3 PUFAs are essential for supporting the body's defences against chronic diseases and CLA may have beneficial protective effects against cancer and inflammatory disorders (Chikwanha et al., 2018). Moreover, a faster growth rate of lambs during the grazing season reduces the risk of having to finish them indoors on a concentrate-based diet, which progressively reduces the nutritional value benefits of pasture-feeding (Aurousseau et al., 2007; Scerra et al., 2011).

Colour and flavour are two important sensory quality traits of lamb meat (Sheath et al., 2001; Prache et al., 2022). Colour is the primary consumer-perceived quality criterion and can make or break a purchase decision (Prache et al., 2022). Pasture-feeding has been shown to reduce lightness (Priolo et al., 2002; Eiras et al., 2022) and increase redness of the meat (Eiras et al., 2022), which can be considered negative from a consumer point of view. These effects are reinforced by an increase in age at slaughter (Prache et al., 2022); however, the effect on meat redness is not linear, as it is strong in the first 120 days of life but then slows down (Calnan et al., 2016). Pasture-fed animals also have a propensity to produce meat with a high ultimate pH (**pHu**), which further darkens the meat (Calnan et al., 2016). A short concentrate-finishing period after pasture-feeding had no effect on meat colour (Eiras et al., 2022). Flavour is also an important quality trait of lamb meat, as an unpleasant experience can deter a consumer from purchasing lamb again; excessive flavour is undesirable in most lamb markets (Schreurs et al., 2008; Watkins et al., 2013; Prache et al., 2022). It is widely recognised that pasture-feeding results in a typical 'pastoral' flavour and a higher risk of excessive flavour (Resconi et al., 2009; Prache et al., 2022). Pastoral flavour has been partly associated with a high concentration of 3-methyl-indole (or skatole, a faecal-smelling compound) in meat fat (Sheath et al., 2001; Young et al., 2003; Schreurs et al., 2008; Watkins et al., 2013). This effect of pasture-feeding has been attributed to enhanced ruminal degradation of the amino acid tryptophan due to the typically high protein content and high ratio of protein/readily-digestible carbohydrate in pasture diets (Young et al., 2003). This pastoral flavour is stronger when pasture herbage is younger and therefore richer in proteins (Young et al., 2003; Schreurs et al., 2008; Watkins et al., 2013). A short concentrate-finishing period after pasture-feeding strongly reduces fat skatole concentration (Gkarane et al., 2019; Eiras et al., 2022).

The most important commercial quality attributes of lamb carcasses are weight, conformation and fatness (with a preference for EUROP classes 2 and 3). In addition to breed and sex, lamb birth weight is an important factor for carcass weight and fatness (Prache et al., 2022), with lighter lambs at birth being fatter at a given BW (Villette and Thériez, 1981). Firmness and colour of fat cover are also important carcass sensory quality traits, with a preference for firm, light fat (Prache and Bauchart, 2015). Pasture-feeding increases the lightness of fat cover (Priolo et al., 2002; Rivaroli et al., 2019); it has also been shown to increase yellowness of fat cover due to an accretion of the carotenoids found in pasture herbage (Priolo et al., 2002), although this is not always observed (Rivaroli et al., 2019; Devincenzi et al., 2019). Pasture-fed lambs have firmer dorsal fat than concentrate-fed lambs (Priolo et al., 2002; Rivaroli et al., 2019) due to lower fat water and low-melting point FA contents (Prache et al., 2022). A short concentrate-finishing period after pasture-feeding had no effect on fat cover firmness (Eiras et al., 2022) but led to a lower fat carotenoid content and therefore fat yellowness, through a dilution phenomenon (Huang et al., 2015).

In the present study, we used a subset of lambs produced in this long-term experiment, to investigate the effects of combining beef cattle and sheep on some lamb carcass and meat sensory quality traits, in order to complete the evaluation of the multi-performance of the corresponding systems.

Material and methods

Experimental design

This study used a subset of lambs produced in a previous long-term experiment, that was designed to test the hypothesis that combining sheep and beef cattle in a pasture-based system would promote the production of grass-fed meat by increasing lamb growth rate at pasture, strengthen system self-sufficiency (Prache et al., 2023) and improve economic and environmental performance (Benoit et al., 2023). Full details of this system-level experiment can be found in Prache et al. (2023). Briefly, we established three grassland-based organic systems as separate farmlets in a mountainous area (at 1 100–1 400 m asl): a mixed system (**MIX**) combining beef cattle and sheep (60:40 cattle:sheep livestock units (**LUs**)), and two monospecific systems, i.e. a beef cattle-only system and a sheep-only system (**SH**), to serve as reference points. All three systems used a similar surface area and stocking rate (LU/ha). Most ewes (Limousine breed) were crossed with Suffolk rams and the remainder were mated with Limousine rams for ewe-lamb replacement.

Lambing and calving were adjusted to grass growth to optimise grazing. All male lambs were castrated in order to facilitate pasture-finishing and avoid untimely mating of female lambs. Lambs were pasture-fed without any supplementation from turn-out to pasture in spring until slaughter, unless they were not ready for slaughter 3–4 weeks before the start of the mating period in mid-October, in which case, they were finished indoors with a concentrate-based diet (concentrate and hay offered *ad libitum*). The concentrate contained 0.87 Unités Fourragères Viande and 159 g CP/kg DM, and comprised 264 g·kg^{-1} faba beans, 243 g·kg^{-1} lucerne, 140 g·kg^{-1} corn, 135 g·kg^{-1} barley, 150 g·kg^{-1} wheat bran, 20 g·kg^{-1} wheat, 30 g·kg^{-1} wheat red shorts,15 g·kg^{-1} calcium carbonate and 3 g·kg^{-1} sodium chloride. All cattle and sheep co-grazed from turn-out to pasture until weaning the lambs, and the lambs then grazed aftermaths until slaughter. Details of the floristic composition of the grassland used can be found in Prache et al. (2023). In brief, grasses, legumes and forbs represented 49, 13 and 37% of grassland area cover, respectively. The decision to supplement adult females with concentrate was based on reaching a target body condition score (**BCS**) at key periods of the reproduction periods (in particular, a BCS of 3.0 at lambing to ensure high lamb BW at birth and high ewe milk production, and avoid the effects of underfeeding during gestation on carcass and meat quality attributes (Villette and Thériez, 1981; Prache et al., 2022)). The concentrate given to ewes during the 37 last days of gestation contained 0.90 Unités Fourragères Lait and 160 g CP/kg DM, and comprised 267 g·kg^{-1} lucerne, 235 g·kg^{-1} faba beans, 155 g·kg^{-1} corn, 150 g·kg^{-1} wheat bran, 145 g·kg^{-1} wheat, 30 g·kg^{-1} wheat red shorts, 14 g·kg^{-1} calcium carbonate and 3 g·kg^{-1} sodium chloride. The concentrate given to ewes between lambing and turn-out to pasture contained 0.90 Unités Fourragères Lait and 159 g CP/kg DM, and comprised 250 g·kg^{-1} lucerne, 247 g·kg^{-1} faba beans, 150 g·kg^{-1} wheat bran, 100 g·kg^{-1} corn, 95 g·kg^{-1} barley, 50 g·kg^{-1} bulgur wheat, 45 g·kg^{-1} wheat, 30 g·kg^{-1} wheat red shorts, 6 g·kg^{-1} soybean oil, 23 g·kg^{-1} calcium carbonate, 3 g·kg^{-1} sodium chloride and 1 g·kg^{-1} phosphorus. The decision to treat lambs with anthelmintics was based on mean faecal egg excretion remaining below a certain threshold (full details of the parasite management are given in Prache et al. (2023)).

In the present study, we used all the crossed-castrated male lambs produced during the first experimental year, including those that were finished indoors with a concentrate-based diet at the end of the grazing season. This design allowed us to take into account all between-lamb variability in terms of growth pattern and age at slaughter, and all seasonal variation in pasture herbage characteristics, so as to provide robust information on the effects of combining sheep and beef cattle in a mixed grassland-based system on the lamb carcass and meat sensory quality traits investigated.

Management

There were 33 and 85 crossed Suffolk × Limousine castrated male lambs slaughtered in the MIX and SH systems, respectively. Lambing took place on average on 23 February (from 29 January to 08 March) in the MIX system and 22 February (from 4 February to 13 March) in the SH system, respectively. Turn-out to pasture took place on 4 April in the MIX system and 5 April in the SH system. Number of lambs suckled per ewe was 1.68 in the MIX system vs 1.79 in the SH system. Lambs were weaned on 24 July in the MIX system and 18 July in the SH system. Lambs selected for slaughter had a BW of 40 kg or more and were fat class 2–3, with priority given to fat class. Twelve MIX lambs (36.4%) and nine SH lambs (10.6%) met the criteria for slaughter before weaning and were therefore not weaned before slaughter. All MIX lambs were finished at pasture, whereas one SH lamb had to be finished indoors with a concentrate-based diet at the end of the grazing period; this lamb was switched to the indoor-fed concentrate-based diet on 2 October and was slaughtered on 29 November, so it spent 58 days indoors before slaughter. The lambs were slaughtered in the INRAE-run slaughterhouse at the Herbipôle experimental unit, located 30 km from the experimental site. On arrival, the lambs were immediately electrically stunned and slaughtered by throat-cutting. Evisceration and skinning were performed as per standard commercial practice. The carcasses were then placed in a chiller at 4 °C until 24 h after slaughter.

Measurements

Lambs were weighed at birth, at weaning, and on the day of slaughter, and at every two-week interval between these key dates (full weight). Herbage samples were taken from each plot to be grazed by the lambs from turn-out to pasture until 11 August, then dried at 60 °C for 72 h, milled through a 1-mm mesh, and bulked per plot. The bulked material from each plot was then used to determine net energy value (Unités Fourragères Viande/kg DM) and CP (g/kg DM) content. Full details of the measurements and methods used are given in Prache et al. (2023).

Carcass characteristics and fat sampling

After chilling, the carcasses were weighed and graded for conformation and fatness using a 15-point scale, as described in Eiras et al. (2022). Kidney fat weight and thickness of dorsal fat cover over the last thoracic rib were measured. A subsample of kidney fat was wrapped and vacuum-packed in a sealable polyamide bag, then snap-frozen, and stored at −20 °C until chemical analysis.

Longissimus thoracis et lumborum muscle and dorsal fat characteristics and sensory quality attributes

The pHu and colour coordinates of LTL muscle were measured as described in Eiras et al. (2022). Dorsal fat colour and firmness were measured as described in Devincenzi et al. (2019).

Fat skatole and indole concentration analysis

Kidney fat skatole and indole concentrations were determined by HPLC using the procedure given in Eiras et al. (2022). Concentrations were expressed in μg per gram of the lipid fraction from adipose tissue. The limit of detection was 0.03 μg/g liquid fat.

Statistical analysis

Data for lamb performance (BW at birth, weaning and slaughter; average daily gain between birth and weaning (**ADG$_{bw}$**); average daily gain between birth and slaughter (**ADG$_{bs}$**); age at slaughter), carcass characteristics (carcass weight, conformation and degree of fatness; dorsal fat thickness; kidney fat weight), carcass sensory quality attributes (colour coordinates and firmness of dorsal fat), meat quality attributes (LTL pHu and colour coordinates) were all analysed using ANOVA with system as fixed factor, following test for normality (Shapiro-Wilk test) and homogeneity of variances (*F*-test). As the variance for dorsal fat lightness and LTL muscle redness, yellowness, chroma and hue angle significantly differed between systems and was not stabilised using log-transformation, these variables were analysed using non-parametric statistics (Wilcoxon W test). The between-system differences in dorsal fat and LTL muscle colour (ΔE_{ab}^*) were calculated as described in Devincenzi et al. (2019). As the residuals for kidney fat skatole and indole concentrations were not normally distributed, between-system differences in kidney fat skatole and indole concentrations were analysed using non-parametric statistics (Wilcoxon W test). Seasonal variability of kidney fat skatole and indole concentrations within each system was analysed using non-parametric statistics (Kruskall-Wallis test, pairwise comparisons being performed using Wilcoxon W test with a Bonferroni correction). A chi-squared test was used to analyse between-system difference in the seasonal distribution of lamb slaughter dates, using time periods that allowed for at least six lambs per period in each system. The animal served as statistical unit.

Results

The net energy value and CP content of the pasture herbage were high and similar for the two systems (0.90 vs 0.92 Unités Fourragères Viande/kg DM for MIX vs SH and 161 vs 169 g/kg DM for MIX vs SH, respectively). Lamb BW at birth and at slaughter did not differ between systems (Table 1), but lamb BW at weaning, ADG_{bw} and ADG_{bs} were higher in MIX system than in SH system ($P < 0.001$ for all variables). Age at slaughter was therefore logically lower in MIX system than in SH system ($P < 0.001$). The distribution of lamb slaughter dates differed between systems ($P < 0.001$), with a higher proportion of lambs slaughtered between July and August 15 in MIX than in SH (51.5 vs 17.6%) and a lower proportion of lambs slaughtered in September and October-November in MIX than in SH (30.3 vs 40.0% and 18.2 vs 30.6%, respectively) (Fig. 1). There were no significant between-system differences in carcass weight, conformation and degree of fatness and in kidney fat weight and dorsal fat thickness (Table 2). Carcass degree of fatness averaged 7.54 and 7.43 in MIX and SH systems, respectively, which corresponds to 3- in the EUROP classification.

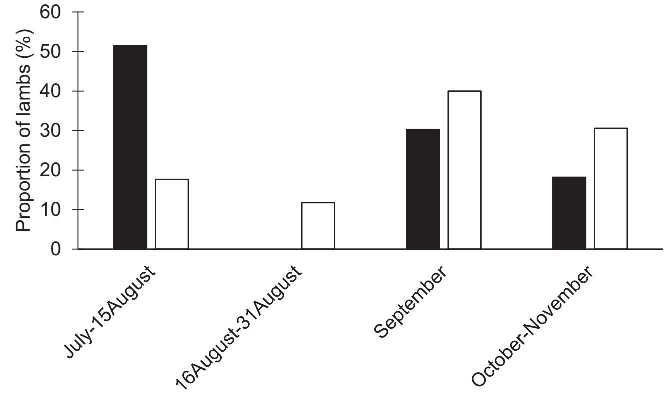

Fig. 1. Distribution of lambs slaughter dates as affected by farming system. Solid and open symbols refer to the mixed system combining sheep and beef cattle and the sheep-only system, respectively.

Kidney fat skatole and indole concentrations

Kidney fat skatole concentration was higher in MIX than in SH ($P < 0.05$), median value reaching 0.15 µg/g liquid fat in MIX vs 0.11 µg/g liquid fat in SH (Fig. 2). Kidney fat indole concentration was not significantly different between systems, median value reaching 0.06 µg/g liquid fat in MIX vs 0.08 µg/g liquid fat in SH (Fig. 3). Fig. 4 gives the proportion of lambs in the different classes of kidney fat skatole concentration for MIX and SH.

In both systems, we observed seasonal variability in kidney fat skatole concentration ($P < 0.05$ and $P < 0.001$ for MIX and SH systems, respectively) (Figs. 5 and 6), but not in kidney fat indole concentration. Indeed, kidney fat skatole concentration was higher in lambs slaughtered between July and August 15 than in lambs slaughtered in the other periods. In addition, in the SH system only, we observed that kidney fat skatole concentration was higher in lambs slaughtered in October than in lambs slaughtered between August 16 and August 31 ($P < 0.05$) or between September 1 and September 15 ($P < 0.001$).

Sensory attributes of subcutaneous dorsal fat and longissimus thoracis et lumborum muscle

Firmness of subcutaneous dorsal fat was not significantly different between systems (Table 3), but MIX lambs tended to have firmer fat ($P = 0.064$). Dorsal fat colour coordinates did not differ between systems. LTL muscle pHu was not significantly different between systems (Table 4) and ranged from 5.18 to 5.45 in MIX lambs and from 5.20 to 5.64 in SH lambs. LTL muscle lightness, redness and hue angle were not significantly different between systems, but LTL muscle yellowness and chroma were lower in MIX vs SH lambs ($P < 0.025$ and $P < 0.05$, respectively).

Discussion

Lambs had very similar carcass fatness, kidney fat weight and dorsal fat thickness in the two systems, thus avoiding a potential confounding effect on the meat and carcass sensory quality attributes investigated in this study (Prache et al., 2022). The between-system difference in carcass weight was borderline statistically significant but the difference was very small in absolute terms (18.10 kg in MIX lambs vs 17.96 kg in SH lambs). Lamb BW at birth was similar between the MIX and SH systems and was therefore not a confounding factor for carcass weight (Prache et al., 2022). The number of lambs suckled per ewe was also not different between MIX and SH systems and was therefore not a confounding factor for lamb ADG_{bw} and age at slaughter. Therefore, the lower lamb age at slaughter in MIX vs SH was exclusively driven by the higher lamb growth rate from birth until slaughter in MIX vs SH, more likely due to a lower level of parasite burden than to a better nutritive value of pasture herbage, as the nutritive value of pasture herbage was similar between the two systems, while the number of anti-parasite drenches used tended to be lower in the MIX system than in the SH system (Prache et al., 2023). Note that mean lamb BW at birth was high in both systems (more than 5 kg), which is key for promoting good growth for grass-fed lamb meat (Prache and Thériez, 1988) and satisfactory carcass commercial quality attributes, especially weight and degree of fatness (Villette and Thériez, 1981; Prache and Bauchart, 2015; Prache et al., 2022).

One of the key findings of this study is that the median value for kidney fat skatole concentration was higher in MIX lambs than in

Table 1
Lamb performance stratified by farming system.

System	Mixed[1]	Monospecific[2]	SEM	*P*-value
BW at birth (kg)	5.40	5.26	0.072	0.403
BW at weaning (kg)	37.39	30.04	0.570	<0.001
BW at slaughter (kg)	43.24	42.76	0.268	0.429
Age at slaughter (days)	150	173	2.8	<0.001
ADG_{bw}[3] (g)	267	211	4.6	<0.001
ADG_{bs}[4] (g)	264	224	4.0	<0.001

[1] System combining sheep and beef cattle.
[2] Sheep-only system.
[3] Average daily gain between birth and weaning.
[4] Average daily gain between birth and slaughter.

Table 2
Lamb carcass characteristics stratified by farming system.

System	Mixed[1]	Monospecific[2]	SEM	*P*-value
Cold carcass weight (kg)	18.10	17.96	0.118	0.057
Carcass conformation	7.09	6.79	0.122	0.427
Carcass fatness	7.54	7.43	0.145	0.734
Kidney fat weight (g)	278	262	8.8	0.427
Dorsal fat thickness (mm)	3.3	3.3	0.09	0.853

[1] System combining sheep and beef cattle.
[2] Sheep-only system.

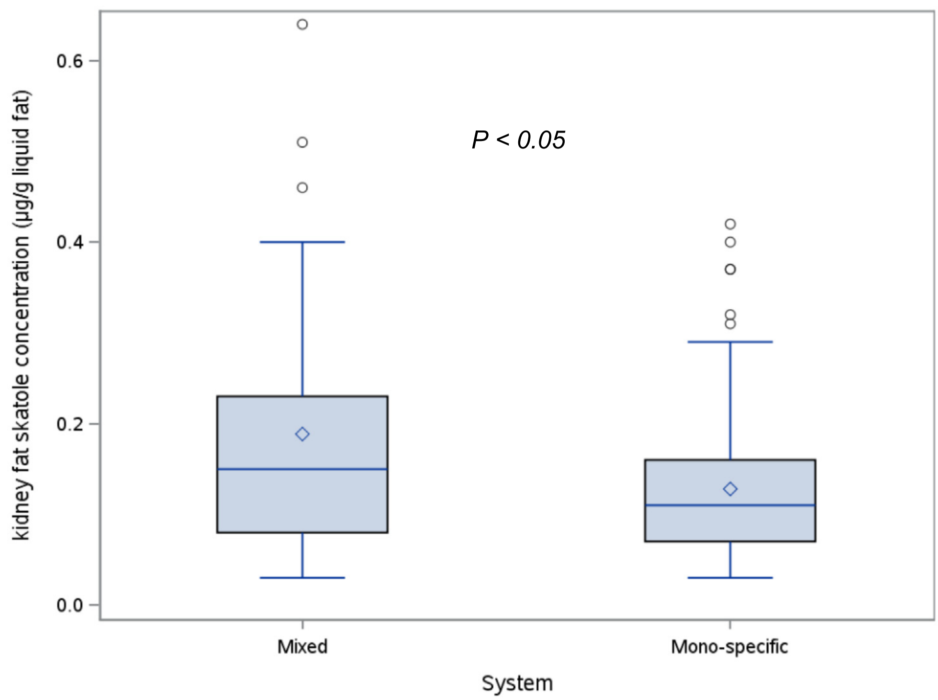

Fig. 2. Box-plot representation of kidney fat skatole concentration in lambs as affected by farming system. The mixed system combines sheep and beef cattle, and the monospecific system is a sheep-only system. The upper edge of the box indicates the 75th percentile of the dataset, the line in the box indicates the median value, the diamond in the box indicates the mean value, and the lower edge indicates the 25th percentile of the dataset. The circles represent outliers.

SH lambs. Note that kidney fat weight was very similar in MIX and SH lambs, so there was no risk of a potential dilution effect. There was seasonal variation in kidney fat skatole concentration in both systems. Kidney fat skatole concentration was highest between July and August 15, this period covering the time when lambs started to graze the pasture herbage regrowths after mowing, and thus the period when the herbage on these pastures was youngest. Previous research has reported greater skatole synthesis (Schreurs et al., 2007a) and more intense pastoral flavour when grass is younger (Schreurs et al., 2008; Watkins et al., 2013). Furthermore, Young et al. (2003) compared pasture-fed lambs slaughtered at 132 days vs 232 days and found that fat skatole concentration was twice as high in younger lambs. The between-system difference in kidney fat skatole concentration observed in the present study was therefore probably due to a difference in lamb age at slaughter inducing a difference in the distribution of lamb slaughterings at different periods in the season. In the present study, 51.5% of MIX lambs were slaughtered during the period 1 July–15 August, when fat skatole concentration was highest vs only 17.6% of SH lambs. Given that tryptophan is the precursor of skatole (Schreurs et al., 2007b; 2008), higher levels of this amino acid in pasture herbage may account for greater skatole production in the rumen and, consequently, greater skatole storage in kidney fat (Schreurs et al., 2007c; 2007d). Unfortunately, we did not collect pasture herbage after August 11 to support the hypothesis that the between-period difference in kidney fat skatole concentration could be explained by a variation in the chemical composition, and in particular the CP content, of the pasture herbage. The between-system difference in proportion of lambs that were finished indoors at the end of the grazing season was unlikely to be a major factor affecting kidney fat skatole concentration in the present study, as only one SH lamb out of 85 was finished indoors on a concentrate-based diet. However, this lamb had no detectable kidney fat skatole, and this effect could become greater if the proportion of lambs that are concentrate-finished increases, as observed in certain years in this long-term experiment (up to 18% crossed-castrated male SH lambs were concentrate-finished; Prache et al., 2023). Several farming practices have proven to effectively reduce fat skatole concentration and thus mitigate over-intense flavour in pasture-fed lamb meat (Schreurs et al., 2008; Rivaroli et al., 2019; Del Bianco et al., 2021; Gkarane et al., 2019; Eiras et al., 2022), but note that all of these practices reduce farming system self-sufficiency, which is contrary to the objective of this long-term experiment.

Dorsal fat firmness was between medium and firm, and the mean value observed in the present study was close to the mean value previously observed in pasture-fed lambs by Priolo et al. (2002). Dorsal fat firmness tended to be higher in MIX than in SH

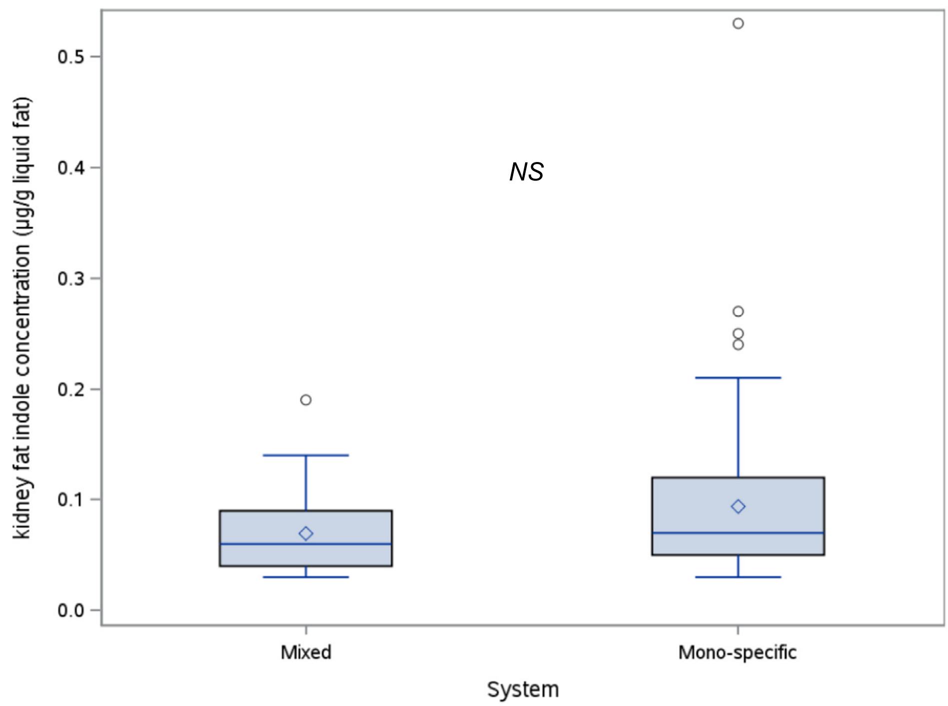

Fig. 3. Box-plot representation of kidney fat indole concentration in lambs as affected by farming system. The mixed system combines sheep and beef cattle, and the monospecific system is a sheep-only system. The upper edge of the box indicates the 75th percentile of the dataset, the line in the box indicates the median value, the diamond in the box indicates the mean value, and the lower edge indicates the 25th percentile of the dateset. The circles represent outliers.

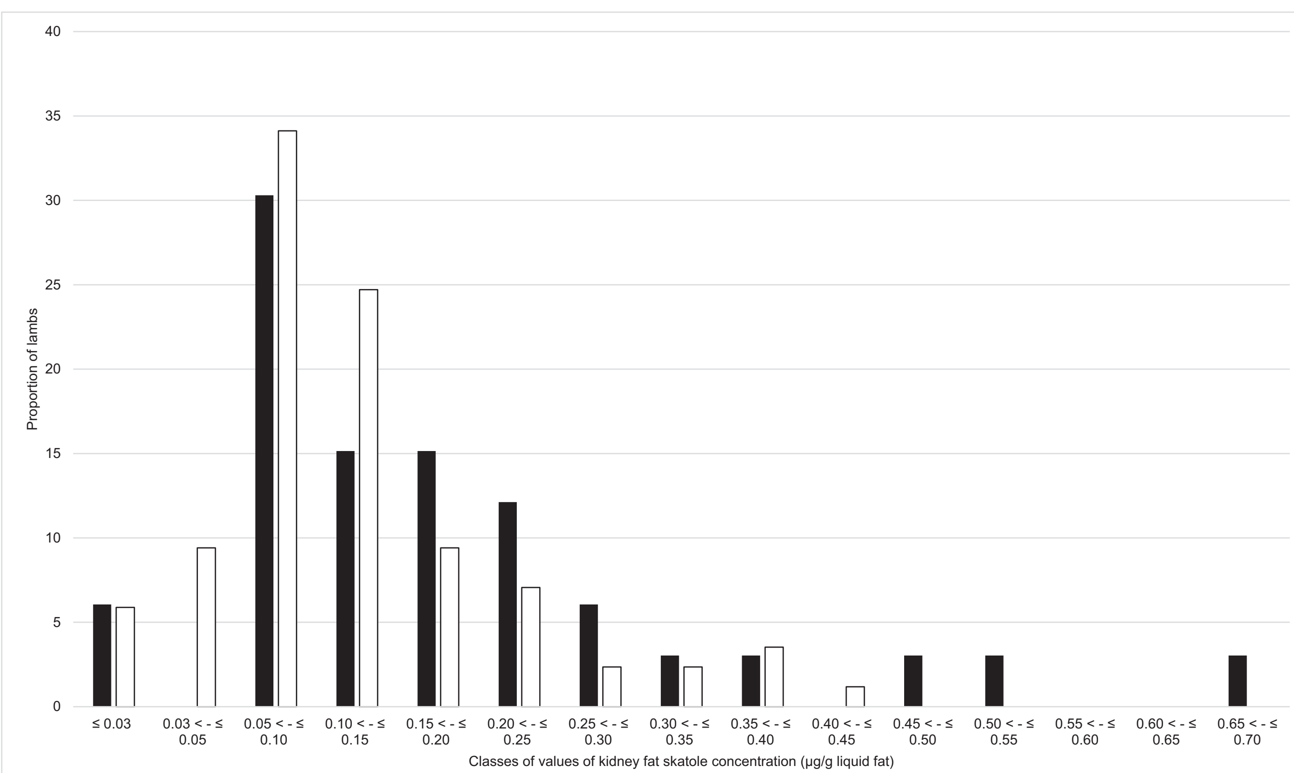

Fig. 4. Proportion of lambs in the different classes of kidney fat skatole concentration as affected by farming system. Solid and open symbols refer to the mixed system combining sheep and beef cattle and the sheep-only system, respectively.

lambs, but the difference was small. This could be due to a higher proportion of lambs slaughtered before weaning in the MIX system than in the SH system (36.4 vs 10.6%), as ADG_{bw} was higher in MIX system lambs than SH system lambs. Longer suckling is actually beneficial for fat cover firmness, as milk lipids are rich in saturated FA (Prache et al., 2022). Concentrate-finishing can reduce dorsal fat

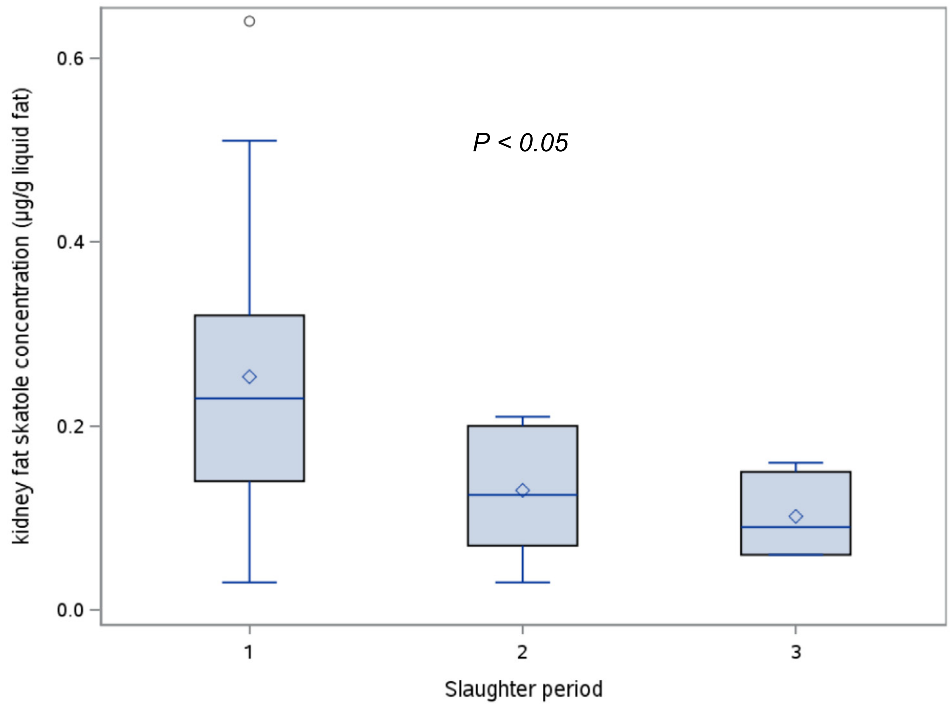

Fig. 5. Box-plot representation of kidney fat skatole concentration in lambs as a function of slaughter period in the mixed system combining sheep and beef cattle. Periods 1, 2 and 3 refer to July–15 August, 01 September–15 September and October, respectively. The upper edge of the box indicates the 75th percentile of the dataset, the line in the box indicates the median value, the diamond in the box indicates the mean value, and the lower edge indicates the 25th percentile of the dataset. The circles represent outliers. Pairwise comparisons of kidney fat skatole concentration among slaughter periods yielded the following results: Period 1 > Periods 2 and 3 ($P < 0.05$ for both pairwise comparisons). Period 2 = Period 3.

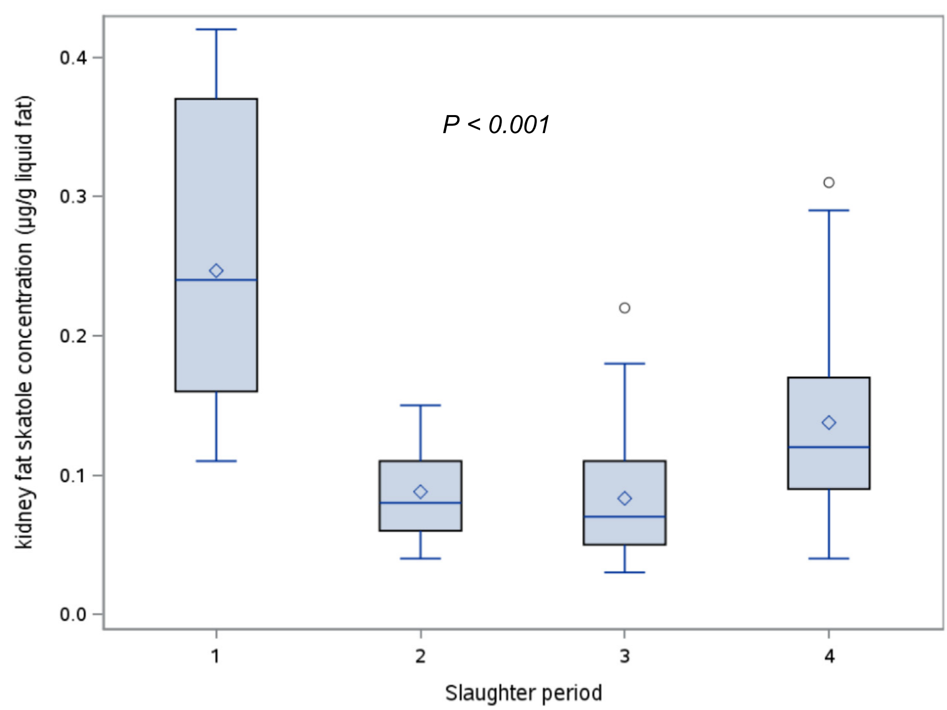

Fig. 6. Box-plot representation of kidney fat skatole concentration in lambs as a function of slaughter period in the sheep-only system. Periods 1, 2, 3 and 4 refer to July-15 August, 16 August–31 August, 01 September–15 September and October, respectively. The upper edge of the box indicates the 75th percentile of the dataset, the line in the box indicates the median value, the diamond in the box indicates the mean value, and the lower edge indicates the 25th percentile of the dataset. The circles represent outliers. Pairwise comparisons of kidney fat skatole concentration among slaughter periods yielded the following results: Period 1 > Periods 2, 3 and 4 ($P < 0.001$ for all pairwise comparisons). Period 4 > Periods 2 ($P < 0.05$) and 3 ($P < 0.001$). Period 2 = Period 3.

Table 3
Sensory quality attributes of carcass dorsal fat in lambs stratified by farming system.

System	Mixed[1]	Monospecific[2]	SEM	*P*-value
Firmness	10.48	9.66	0.200	0.064
Lightness (L^*)	72.64[3]	73.46[3]	–[3]	0.621[3]
Redness (a^*)	1.15	1.18	0.159	0.914
Yellowness (b^*)	12.68	13.18	0.271	0.401
Chroma	12.83	13.30	0.277	0.443
Hue angle	85.63	86.11	0.694	0.753

[1] System combining sheep and beef cattle.
[2] Sheep-only system.
[3] Median value given and SEM value not given, as the variance for L* of dorsal fat differed between systems; *P*-value was computed based on non-parametric Kruskall-Wallis test.

Table 4
Longissimus thoracis et lumborum muscle characteristics in lambs stratified by farming system.

System	Mixed[1]	Monospecific[2]	SEM	*P*-value
Ultimate pH	5.33	5.35	0.001	0.264
Lightness (L^*)	31.80	31.57	0.379	0.713
Redness (a^*)	11.20[3]	11.36[3]	–[3]	0.116[3]
Yellowness (b^*)	13.15[3]	14.08[3]	–[3]	0.021[3]
Chroma	17.24[3]	18.13[3]	–[3]	0.033[3]
Hue angle	49.85[3]	48.60[3]	–[3]	0.282[3]

[1] System combining sheep and beef cattle.
[2] Sheep-only system.
[3] Median value given and SEM value not given, as the variance differed between systems; *P*-value was computed based on non-parametric Kruskall-Wallis test.

firmness due to a decrease in ruminal pH and an increase in propionate production (Prache et al., 2022), but this effect is not always significant (Eiras et al., 2022). In the present study, only one out of 85 SH lambs was concentrate-finished at the end of the grazing season, so this effect was likely of little importance, but it could become greater if the proportion of lambs that are concentrate-finished increases, as discussed earlier (Prache et al., 2023).

There was no occurrence of high LTL muscle pHu in either system, and any between-system differences in LTL muscle colour coordinates were only minor. Yellowness and consequently chroma were lower in MIX system lambs than in SH system lambs, but the underlying mechanism remains unclear. These differences may be visible to the naked eye, as the ΔE_{ab}^* value was 1.34, i.e. just above the value of 1 considered as the threshold for perceiving a colour difference in meat (Hill et al., 1997). The values observed in the present study for LTL muscle colour coordinates were similar (lightness and redness) or a bit higher (yellowness) than the values reported by Eiras et al. (2022) in pasture-fed Romane-breed lambs slaughtered at a similar age.

This study used a subset of lambs produced in a four-year experiment, i.e. all the castrated Suffolk × Limousine crossbred male lambs produced in the first year. This raises the question of whether these results can be generalised across the four experimental years and beyond. Given that pasture and animal management were similar in the four experimental years (Prache et al., 2023), there may be two reasons for potential between-year variations in fat skatole concentrations. First, there may be between-year seasonal variations in the distribution of slaughter dates, as we found seasonal variation in fat skatole concentrations. Second, there may be between-year variations in the proportion of lambs concentrate-finished at the end of the grazing season, as concentrate-finishing has been shown to dramatically reduce fat skatole concentration (Gkarane et al., 2019; Eiras et al., 2022). We found no significant between-year difference in proportion of lambs slaughtered before vs after 15 August (which is the period where fat skatole concentration was the highest vs the lowest), for both MIX and SH lambs, and so it is likely that the between-system variation due to the between seasonal variation in fat skatole content is reproducible from year to year. Analysis pooling all four experimental years showed that the proportion of lambs slaughtered before 15 August reached 40.2% in the MIX system vs 16.1% in the SH system ($P < 0.001$). Note that these proportions were 51.5% in the MIX system and 17.9% in the SH system in the first experimental year studied in the present study. Conversely, the proportion of SH lambs that had to be finished indoors with a concentrate-based diet at the end of the grazing season was much lower in the first experimental year (1.2%) than in the next three years (16.0%; $P < 0.005$–$P < 0.001$), which showed no significantly between-year difference. Moreover, all MIX lambs produced over the 4 years were pasture-finished, except in the third year, where 3.8% of MIX lambs had to be finished indoors. Given the effect of indoor concentrate-finishing (Eiras et al., 2022), this would be expected to accentuate the between-system difference in fat skatole concentration for the last three experimental years, namely a higher fat skatole concentration in the MIX system than in the SH system.

Conclusion

Combining sheep and beef cattle within a pasture-based mixed system promotes the production of grass-fed lamb meat and has advantages for system self-sufficiency, economic and environmental performance and feed-food competition. However, our results show higher fat skatole concentrations in lambs from the mixed system combining sheep and beef cattle, which could increase the risk of excessive flavour in lamb meat and ultimately reduce consumer interest. Other between-system differences were found in dorsal fat firmness and *longissimus thoracis et lumborum* muscle colour, but were minor.

Ethics approval

All procedures used in this study were approved by the C2EA-02 institutional animal care and use committee (APAFIS#1417-2015081011477291 v3 and APAFIS#24191-2015043014541577 v4).

Data and model availability statement

None of the data used has been deposited in an official repository.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

None.

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References

Aurousseau, B., Bauchart, D., Faure, X., Galot, A.L., Prache, S., Micol, D., Priolo, A., 2007. Indoor fattening of lambs raised on pasture: (1) Influence of stall finishing duration on lipid classes and fatty acids in the longissimus thoracis muscle. Meat Science 76, 241–252.

Barn, J., Thüer, S., Holinger, M., Oberhänsli, T., Leubin, M., Leiber, F., Werne, S., 2022. Performance and parasitological parameters of steers sequentially grazed with lambs. Veterinary Parasitology 302, 109645.

Bauchart, D., Oueslati, K., Thomas, A., Ballet, J., Prache, S., 2012. Un mode de conduite biologique et un niveau élevé d'herbe améliorent la qualité nutritionnelle des acides gras de la viande chez l'agneau engraissé au pâturage. In: Proceedings of the 14èmes Journées Scientifiques sur le Muscle et les Technologies de la Viande (JSMTV), 13–14 Novembre 2012, Caen, France, pp. 23–24.

Benoit, M., Vazeille, K., Jury, C., Troquier, C., Veysset, P., Prache, S., 2023. Combining beef cattle and sheep in an organic system. II. Benefits for economic and environmental performance. Animal 17, 100759.

Calnan, H., Jacob, R.H., Petick, D.W., Gardner, G.E., 2016. Production factors influence fresh *longissimus* colour more than muscle traits such as myoglobin concentration and pH. Meat Science 119, 41–50.

Chikwanha, O.C., Vahmani, P., Muchenje, V., Dugan, M.E.R., Mapiye, C., 2018. Nutritional enhancement of sheep meat fatty acid profile for human health and wellbeing. Food Research International 104, 25–38.

D'Alexis, S., Sauvant, D., Boval, M., 2014. Mixed grazing systems of sheep and cattle to improve liveweight gain: a quantitative review. Journal of Agricultural Science 152, 655–666.

Del Bianco, S., Natalello, A., Luciano, G., Valenti, B., Campidonico, L., Gkarane, V., Monahan, F., Biondi, L., Favotto, S., Sepulcri, A., Piasentier, E., 2021. Influence of dietary inclusion of tannin extracts from mimosa, chesnut and tara on volatile compounds and flavour in lamb meat. Meat Science 172, 108336.

Devincenzi, T., Prunier, A., Meteau, K., Prache, S., 2019. How does barley supplementation in lambs grazing alfalfa affect meat sensory quality and authentication? Animal 13, 427–434.

Eiras, C.E., Prunier, A., Méteau, K., do Prado, I.N., Prache, S., 2022. Is a short concentrate-finishing period in lambs raised on alfalfa pasture effective at reducing fat indoles contents and lightening meat colour? Animal 16, 100610.

Gkarane, V., Brunton, N.P., Allen, P., Gravador, R.S., Claffey, N.A., Diskin, M.G., Fahey, A.G., Farmer, L.J., Moloney, A.P., Alcalde, M.J., Murphy, P., Monahan, F.J., 2019. Effect of finishing diet and duration on the sensory quality and volatile profile of lamb meat. Food Research International 115, 54–64.

Hill, B., Roger, T., Vorhagen, F.W., 1997. Comparative analysis of the quantization of color spaces on the basis of the CIELAB color-difference formula. ACM Transactions on Graphics 16, 109–154.

Huang, Y., Andueza, D., de Oliveira, L., Zawadzki, F., Prache, S., 2015. Visible spectroscopy on carcass fat combined with chemometrics to distinguish pasture-fed, concentrate-fed and concentrate-finished pasture-fed lambs. Meat Science 101, 5–12.

Jerrentrup, J.S., Komainda, M., Seither, M., Cuchillo-Hilario, M., Wrage-Möning, N., Isselstein, J., 2020. Diverse swards and mixed-grazing of cattle and sheep for improved productivity. Frontiers in Sustainable Food Systems 3.

Joly, F., Note, P., Barbet, M., Jacquiet, P., Faure, S., Benoit, M., Dumont, B., 2022. Parasite dilution improves lamb growth more than does the complementary of forage niches in a mesic pasture grazed by sheep and cattle. Frontiers in Animal Science 3, 997815.

Liu, J., Ellies-Oury, M.P., Pannier, L., Gruffat, D., Durand, D., Noel, F., Sepchat, B., Legrand, I., Prache, S., Hocquette, J.F., 2022. Carcass characteristics and beef quality of young grass-fed Angus x Salers bovines. Foods 11, 2493.

Liu, J., Pannier, L., Ellies-Oury, M.P., Legrand, I., Noel, F., Sepchat, B., Prache, S., Pethick, D., Hocquette, J.F., 2023. French consumer evaluation of eating quality of Angus x Salers beef: Effects of muscle cut, muscle ageing, muscle slicing and ageing. Meat Science 197, 109079.

Martin, G., Barth, K., Benoit, M., Brock, C., Destruel, M., Dumont, B., Grillot, M., Hübner, S., Magne, M.A., Moerman, M., Mosnier, C., Parsons, D., Ronchi, B., Schanz, L., Steinmetz, L., Werne, S., Winckler, C., Primi, R., 2020. Potential of multi-species livestock farming to improve the sustainability of livestock farms: a review. Agricultural Systems 181, 102821.

Prache, S., Bauchart, D., 2015. Lamb meat and carcass quality: main criteria of interest. INRA Productions Animales 28, 105–110.

Prache, S., Thériez, M., 1988. Lamb production at pasture. INRA Productions Animales 1, 25–33.

Prache, S., Schreurs, N., Guillier, L., 2022. Review: Factors affecting sheep carcass and meat quality attributes. Animal 16, 100330.

Prache, S., Vazeille, K., Chaya, W., Sepchat, B., Note, P., Sallé, G., Veysset, P., Benoit, M., 2023. Combining beef cattle and sheep in an organic system. I. Co-benefits for promoting the production of grass-fed meat and strengthening self-sufficiency. Animal 17, 100758.

Priolo, A., Micol, D., Agabriel, J., Prache, S., Dransfield, E., 2002. Effect of grass or concentrate feeding systems on lamb carcass and meat quality. Meat Science 62, 179–185.

Resconi, V.C., Campo, M.M., Font-i-Furnols, M., Montossi, F., Sañudo, C., 2009. Sensory evaluation of castrated lambs finished on different proportions of pasture and concentrate feeding systems. Meat Science 83, 31–37.

Rivaroli, D., Prunier, A., Meteau, K., do Prado, I.N., Prache, S., 2019. Tannin-rich sainfoin pellet supplementation reduces fat volatile indoles content and delays digestive parasitism in lambs grazing alfalfa. Animal 13, 1883–1890.

Scerra, M., Luciano, G., Caparra, P., Foti, F., Cilione, C., Giorgi, A., Scerra, V., 2011. Influence of stall finishing duration of Italian Merino lambs raised on pasture on intramuscular fatty acid composition. Meat Science 89, 238–242.

Schreurs, N.M., McNabb, W.C., Tavendale, M.H., Lane, G.A., Barry, T.N., Cummings, T., Fraser, K., Lopez-Villalobos, N., Ramirez-Restrepo, C.A., 2007a. Skatole and indole concentration and the odour of fat from lambs that had grazed perennial ryegrass/white clover pasture or *Lotus corniculatus*. Animal Feed Science and Technology 138, 254–271.

Schreurs, N.M., Tavendale, M.H., Lane, G.A., Barry, T.N., Lopez-Villalobos, N., McNabb, W.C., 2007b. Controlling the formation of indole and skatole in in vitro rumen fermentations using condensed tannin. Journal of the Science of Food and Agriculture 87, 887–899.

Schreurs, N.M., Tavendale, M.H., Lane, G.A., Barry, T.N., McNabb, W.C., Cummings, T., Fraser, K., Lopez-Villalobos, N., 2007c. The effect of supplementation of a white clover or perennial ryegrass diet with grape seed extract on indole and skatole metabolism and the sensory characteristics of lamb. Journal of the Science of Food and Agriculture 87, 1030–1041.

Schreurs, N.M., Tavendale, M.H., Lane, G.A., Barry, T.N., Lopez-Villalobos, N., McNabb, W.C., 2007d. Effect of different condensed tannin-containing forages, forage maturity and nitrogen fertiliser application on the formation of indole and skatole in *in vitro* rumen fermentations. Journal of the Science of Food and Agriculture 87, 1076–1087.

Schreurs, N.M., Lane, G.A., Tavendale, M.H., Barry, T.N., McNabb, W.C., 2008. Pastoral flavour in meat products from ruminants fed fresh forages and its amelioration by forage condensed tannins. Animal Feed Science and Technology 146, 193–221.

Sheath, G., Coulon, J.B., Young, O., 2001. Grassland management and animal product quality. In: Proceedings of the XIX International Grassland Congress, 11–21 February 2001, Sao Pedro, Sao Paulo, Brazil, pp. 1019–1026.

Villette, Y., Thériez, M., 1981. Influence of birth weight on lamb performance. 2. Carcass and chemical composition of lambs slaughtered at the same weight. Annales de Zootechnie 30, 169–182.

Watkins, P.J., Frank, D., Singh, T.K., Young, O.A., Warner, R.D., 2013. Sheepmeat flavor and the effect of different feeding systems: A review. Journal of Agricultural and Food Chemistry 61, 3561–3579.

Young, O.A., Lane, G.A., Priolo, A., Fraser, K., 2003. Pastoral and species flavour in lambs raised on pasture, lucerne or maize. Journal of the Science of Food and Agriculture 83, 93–104.